

FUNARIA MUHLENBERGII AND *FUNARIA PULCHELLA*
(FUNARIACEAE, BRYOPHYTA) IN HUNGARY

P. ERZBERGER

Belziger Str. 37, D-10823 Berlin, Germany

The distribution of the two moss species *Funaria muhlenbergii* and *F. pulchella* in Hungary has been established by revision of the specimens in BP. Contrary to the picture suggested by the Hungarian literature to date, *F. pulchella* is about as frequent as *F. muhlenbergii*. The records of the species are presented in two maps. Some of the morphological features useful in identification of the species are discussed and in part illustrated. The number of stomata per sporophyte is a good discriminating character that significantly differs between the two species: *F. muhlenbergii* has (43–)72(–101) stomata per capsule, *F. pulchella* (19–)31(–42). An analysis of the collection data reveals that the two species may differ slightly in the time of ripening of the sporophyte, since on average the capsules of *F. muhlenbergii* open about two weeks later than those of *F. pulchella*.

Key words: bryophytes, distribution, *Funaria*, Hungary, morphological characters, taxonomy

INTRODUCTION

The species of the *Funaria muhlenbergii* group were poorly understood before the basic work of CRUNDWELL and NYHOLM (1974), in which three species are recognised: *F. muhlenbergii* Turner, *F. pulchella* Philib. and *F. conica* Spruce, the latter a more strictly Mediterranean species that does not occur in Hungary and will not be considered further.

In earlier works (e.g. LIMPRICHT 1895, MÖNKEMEYER 1927) the names *F. dentata* Crome and *F. mediterranea* Lindb. were in use for the taxa now called *F. muhlenbergii* and *F. pulchella*, respectively (see also Discussion), although, taxonomically, these are synonyms of *F. muhlenbergii*, since their types belong to this species (CRUNDWELL and NYHOLM 1974). Boros and other Hungarian collectors used these older names in herbarium labels, but in his monography, BOROS (1968) follows the taxonomic concept of LOESKE (1929), who considered *F. mediterranea* not to be specifically distinct from *F. dentata* and attributed to it the rank of a variety only. However, BOROS (1968) uses the name *F. muhlenbergii* instead of *F. dentata*, and he considers *F. mediterranea* to be merely a habitat form (“Standortsform”), occurring with the type.

Although in the revision of CRUNDWELL and NYHOLM (1974), three Hungarian specimens are mentioned – two of *F. muhlenbergii* (Vértessomló, Csákberény) and one of *F. pulchella* (railway between Alsógöd and Dunakeszi) –, their concept has up to now not been fully applied to the taxa occurring in Hungary. ORBÁN and

VAJDA (1983) correctly quote the Dunakeszi specimen of *F. pulchella*, but they obviously believed that all of the other "*F. muhlenbergii*" records of BOROS do belong to this species sensu Crundwell and Nyholm. In describing the area of *F. muhlenbergii* they closely follow BOROS (1968), thus implying that *F. muhlenbergii* is widespread, whereas *F. pulchella* is a very rare species in Hungary that has only been collected once near Dunakeszi (ORBÁN and VAJDA 1983). Consequently, RAJCZY (1990) considers *F. pulchella* to be an endangered species ("aktuálisan veszélyeztetett mohafaj") because only one site of occurrence was known.

Doubts about this picture arose, when in spring 2001 the author collected *F. pulchella* in four different locations in Hungary. It was therefore decided, to examine the specimens of the Hungarian Natural History Museum of Budapest (BP).

The results of the revision are presented in this paper. They include comments on the morphological differences between the species as seen in Hungarian material, quantitative data on stomatal number, an investigation of the coincidence between *F. dentata* / *F. mediterranea* and *F. muhlenbergii* / *F. pulchella*, a corrected geographical distribution of the species, and an evaluation with respect to their ecological behaviour, especially the phenology of sporophyte ripening.

MATERIAL AND METHODS

All specimens from the present territory of Hungary labelled *Funaria dentata* Crome or a synonym were obtained from the bryophyte collection of the Hungarian Natural History Museum in Budapest (BP). Four gatherings of the author were also included in part of the study (for a list of specimens see Appendix 1). Specimens were examined by light microscopy and revised according to the features mentioned in CRUNDWELL and NYHOLM (1974).

In order to count the number of stomata, a dry capsule was boiled in 2% KOH solution for some seconds, rinsed in water, cut longitudinally in halves, emptied and mounted in water with the outer surface at the top. Using magnifications between $\times 100$ and $\times 400$, stomata can reliably be detected. In a random sample of 6 specimens of each species a total of 47 capsules (on average 3.9 ± 0.2 capsules per specimen) was examined. Since the data did not fulfil the assumptions of parametric tests, a Mann-Whitney U-test was used for the comparison of the species.

For further analysis, the sample of specimens had to be corrected for duplicates.

The coincidence of earlier determinations (as *F. dentata* and *F. mediterranea*, resp.) with the results of the present revision (in terms of *F. muhlenbergii* and *F. pulchella*, resp.) was tested by χ^2 analysis.

To explore possible differences in phenology of the two species, the time of collection (day, month) was evaluated. However, since the collected plants were not in the same phenological stage, the time of collection could not be used directly, but a correction was applied as detailed in Appendix 2. This results in obtaining from the date of collection an "estimated day of dehiscence" *d* for each specimen (counted in days from the beginning of March), i.e. the day when 50% of all capsules in the

specimen are deoperculate. A mean value of d was then computed for each species separately and the difference in mean was tested for statistical significance using Student's t -test.

Nomenclature of mosses follows CORLEY et al. (1981) and CORLEY and CRUNDWELL (1991), that of liverworts GROLLE and LONG (2000).

RESULTS

Of the 98 specimens obtained from BP one did not represent a species of the *Funaria muhlenbergii* group. Of the remaining 97 specimens, 45 (37 after correction for duplicates) were *F. muhlenbergii* and 52 (39) *F. pulchella*. 70 out of these 97 specimens (72.2%) were collected by Boros, the outstanding personality in Hungarian bryology of the 20th century. A list of the specimens studied, together with the results of the revision, is given in Appendix 1.

It was in all cases possible to name species unambiguously; no intermediates were encountered.

The following morphological characters proved to be the most useful with the Hungarian material (Table 1, Fig. 1):

- (i) the denticulation of the leaf margin in the upper part of the leaf (Fig. 1A, D);
- (ii) the size and shape of the ripe theca (Fig. 1B, E);
- (iii) the ornamentation of the spore surface (Fig. 1C, F).

Table 1. Morphological characters useful in distinguishing between *F. muhlenbergii* and *F. pulchella* (CRUNDWELL and NYHOLM 1974, LIMPRICHT 1859 and own observations).

	<i>Funaria muhlenbergii</i>	<i>Funaria pulchella</i>
Leaf margin	sharply serrate in upper half of leaf by projecting cells; marginal cells usually longer and narrower than adjacent cells	nearly entire to bluntly denticulate by slightly projecting cell ends; marginal cells similar to adjacent cells
Spore surface	coarsely papillose	finely papillose to vermiform
Size and shape of ripe theca	ca 3 mm, oblong-pyriform	ca 2 mm, subglobular-pyriform
Stomatal number (mean \pm s.e.)	71.2 \pm 2.9	30.0 \pm 1.5
Length of terminal cell of leaf apex	up to 450 μ m	up to 280 μ m, but often shorter
Length of seta	7–11 mm	5–8 mm

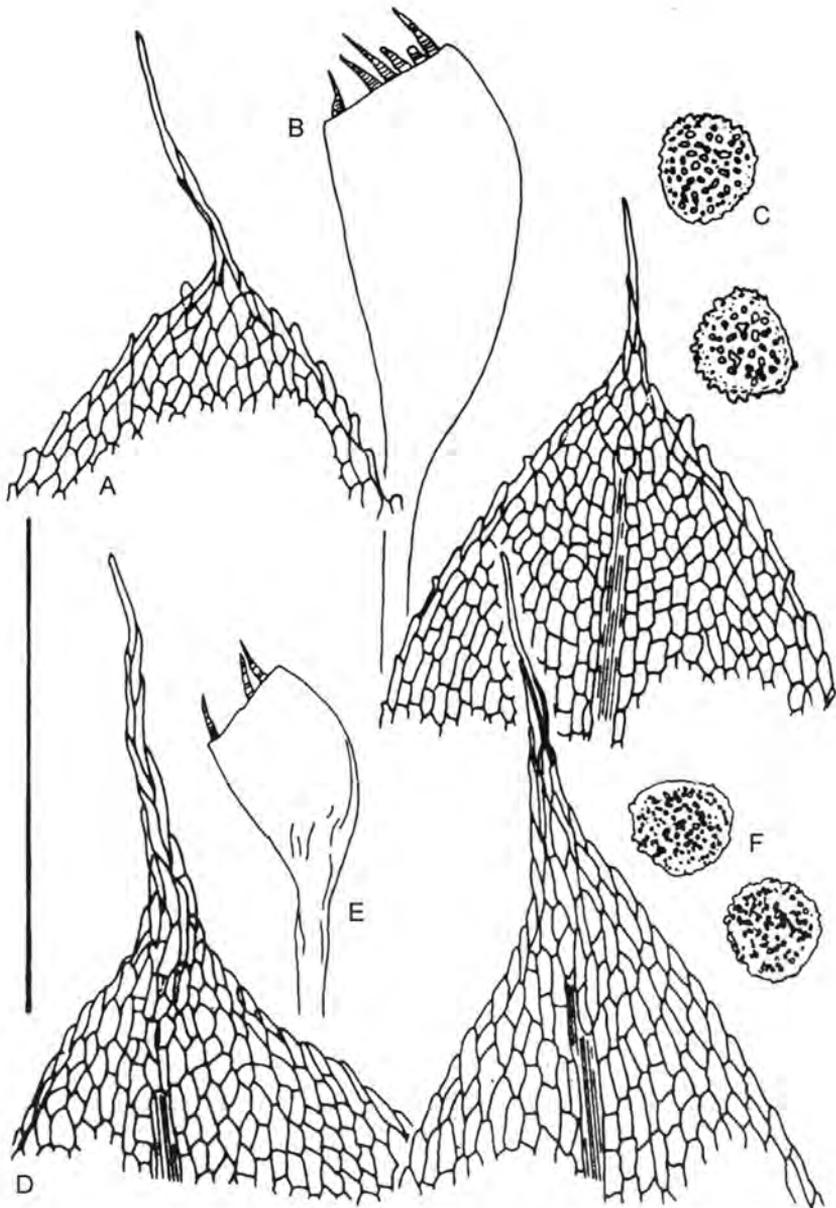


Fig. 1. A–C: *Funaria muhlenbergii*, D–F: *Funaria pulchella*. – A, D: apical part of leaves; B, E: capsules; C, F: spores. Scale bar: leaves: 1 mm; capsules: 3.8 mm; spores: 133 μ m. – A, C from BP 6800 (Pilis Mts, Kétágú-hegy, Kesztlőc); B from BP 114899 (Gerecse Mts, Vörös-hegy, Tatabánya); D from Erzberger 7001 (Gerecse Mts, Pes-kő, Vértestolna); E from BP 114889 (Vértes Mts, Csatornavölgy, Csákberény); F from BP 114914 (Danube valley, railway between Dunakeszi and Alsógöd) (see Appendix 1 for details).

Useful, though not as important as the above-mentioned features, is also the length of the terminal cell of the leaf apex, a character that is excellently illustrated in SMITH (1978) as well as in CRUNDWELL and NYHOLM (1974). Another character mentioned by them is seta length; Hungarian material seems to fall within the ranges reported for British material (Table 1).

Finally, the number of stomata per sporophyte proved to be a good discriminating character (Fig. 2). According to a sample of 6 specimens of each species, stomatal number (minimum – median – maximum) in *F. muhlenbergii* is (43–)72.5(–101), whereas in *F. pulchella* it is (19–)31(–42). The difference is statistically significant ($p < 0.005$) according to the Mann–Whitney U-test ($Z = -5.844$).

In Figure 3, the results of the present revision of Hungarian specimens according to the modern taxonomic concept of the *F. muhlenbergii* group are compared to the names found on the specimen labels that result from out-dated concepts. 30 specimens (81.1%) of the total of 37 specimens revised as *F. muhlenbergii* had been labelled *F. dentata*, but only 7 (18.9%) as *F. mediterranea*. On the other hand, 28 specimens (71.8%) of the total of 39 specimens revised as *F. pulchella* had been labelled *F. dentata*, and 11 (28.2%) as *F. mediterranea*. Although a slightly higher percentage of *F. pulchella* than of *F. muhlenbergii* had

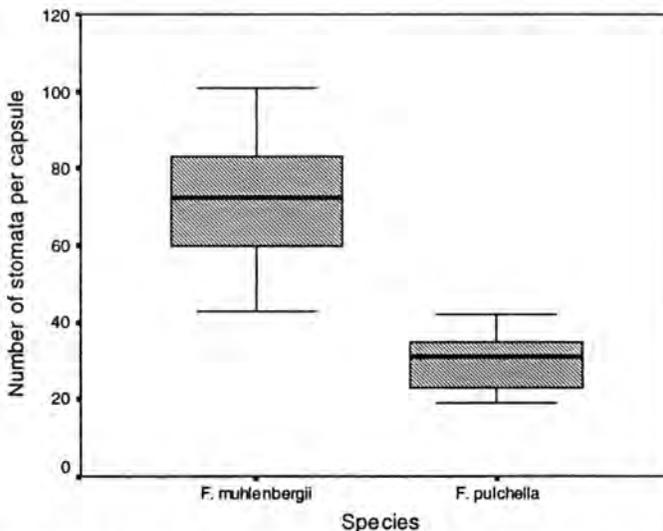


Fig. 2. Boxplot of stomatal number in *Funaria muhlenbergii* and *F. pulchella*. Range and interquartile range (box) with median are depicted. Number of capsules: *F. muhlenbergii*: $n = 26$; *F. pulchella*: $n = 21$.

thus been labelled *F. mediterranea*, the coincidence of the two taxonomic concepts is very poor (Pearson $\chi^2 = 0.906$, $p = 0.341$).

Figures 4 and 5 show the records known at present of *F. muhlenbergii* and *F. pulchella*, respectively, in Hungary. Both species seem to occur predominantly in the Transdanubial part of the Hungarian hills: the Pilis–Buda Mts, the Gerecse Mts and the Vértes Mts west of the Danube. East of the Danube only one isolated record exists of *F. muhlenbergii* and two of *F. pulchella*. Both species also occur in the south of Hungary, in the Villány Mts, and *F. muhlenbergii* in the Mecsek Mts as well. *F. muhlenbergii* seems to extend further to the west: there are records from the Bakony Mts, the Keszthely Mts and the hills north of Lake Balaton. No specimen of *F. pulchella* was seen from these areas.

In those regions where the species occur together, they are sometimes found in the same locations. Examples are Remete-hegy (Máriaremete) in the Pilis-Buda Mts; Pes-kő (Vértistolna) and Vörös-hegy (Tatabánya) in the Gerecse Mts; Lófő-hegy (Várgesztes) and Csatorna-völgy (Csákberény) in the Vértes Mts. One of the specimens of this latter location contains a mixed stand of the two species. This proves that the habitat requirements of *F. muhlenbergii* and *F. pulchella* are very similar, to say the least. According to the information on specimen labels and field observations of the author, both occur in open calcareous grasslands, on thin layers of soil, often rendzina, in crevices or more frequently on ledges of calcareous rock. It is therefore not astonishing, that they are accompanied by nearly the same bryophytes in the specimens studied. The most frequent companions are:

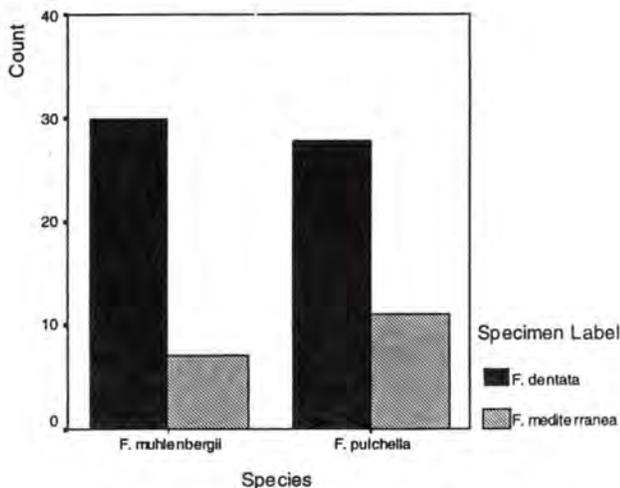


Fig. 3. Comparison of revision results (*F. muhlenbergii* versus *F. pulchella*) with names on specimen labels (*F. dentata* versus *F. mediterranea*). Pearson $\chi^2 = 0.906$, $p = 0.341$.

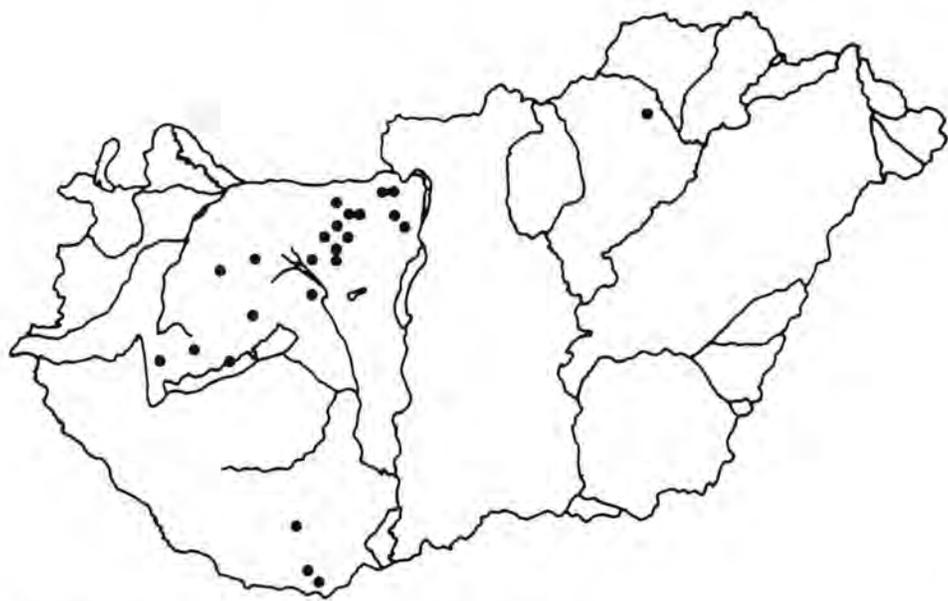


Fig. 4. Records of *Funaria muhlenbergii* in Hungary, according to herbarium specimens revised by the author.

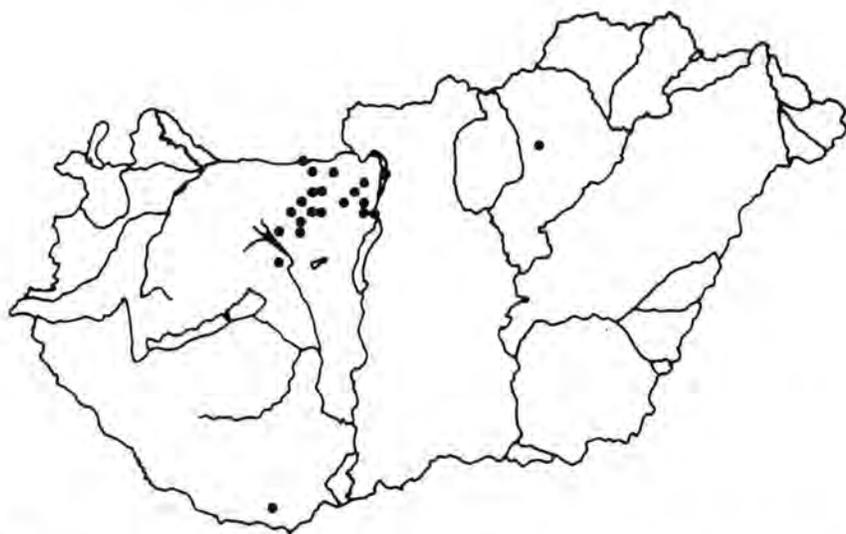


Fig. 5. Records of *Funaria pulchella* in Hungary, according to herbarium specimens revised by the author.

Encalypta vulgaris, *Phascum cuspidatum*, *Mannia fragrans*, *Pleurochaete squarrosa*, *Encalypta streptocarpa* and *Phascum curvicolle*. With the exception of *Encalypta streptocarpa*, these species are typical of the Grimaldion fragrantis Šm. et Had. 1944 (MARSTALLER 1993).

Most specimens of the two species contained considerable numbers of ripe sporophytes, but some few collections consisted of sterile plants or plants with unripe sporophytes still covered by the calyptra. Small numbers of unripe sporophytes were also present in most specimens containing predominantly ripe capsules. Ripening of sporophytes therefore appears to be rather heterogeneous within and among single gatherings. This necessitated the application of a correction to the collection data when the phenology of the two species was to be compared, as detailed in the Methods section and Appendix 2.

The analysis of the collection data shows that sporophytes of both species ripen between March and June, but it also revealed that *F. muhlenbergii* seems to lag behind *F. pulchella* in this respect, when average values are compared (Fig. 6). In *F. muhlenbergii* sporophytes ripen on average about 13 days later (50% deperculate round the 4 May) than in *F. pulchella* (50% deperculate about the 21 April). According to the t-test, the difference in mean day of dehiscence is significant between the species ($t = 2.028$, $df = 74$, $p < 0.05$).

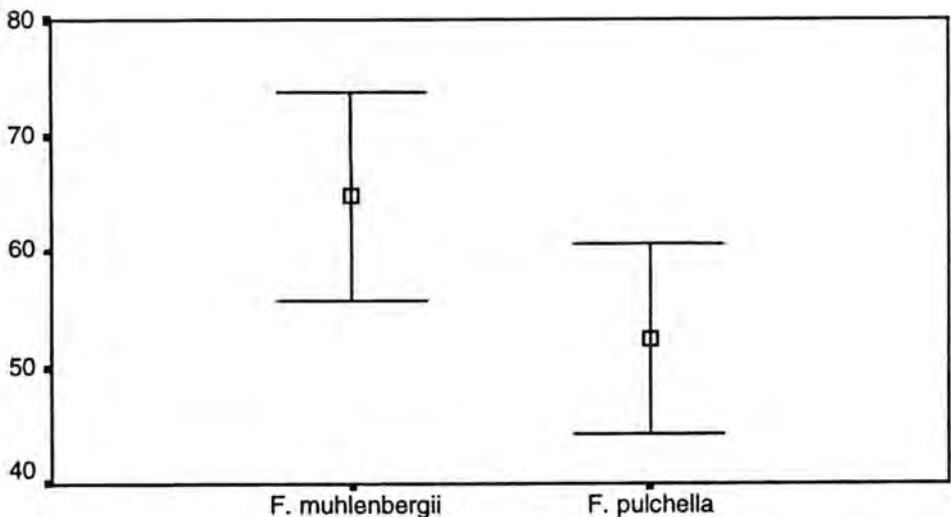


Fig. 6. Time of sporophyte ripening in *Funaria muhlenbergii* and *Funaria pulchella*. Day of dehiscence (counted from 1 March): 50% of sporophytes without lid. Mean \pm 2 standard errors. Number of specimens: *F. muhlenbergii*: $n = 37$; *F. pulchella*: $n = 39$.

DISCUSSION

In the present study, all herbarium specimens in BP of the *F. muhlenbergii* group from Hungary have been assigned to either of the two species *F. muhlenbergii* and *F. pulchella* according to the morphological features detailed in Table 1 and in part illustrated in Figure 1. No intermediate forms have been found.

However, earlier works dealing with this species group in Europe (LOESKE 1929, CRUNDWELL and NYHOLM 1974) come to the conclusion that intermediates do occur and that naming plants is sometimes not possible. In a wider geographical context, the occurrence of other taxa like *F. convexa* or the recently re-evaluated *F. durieui* Bescherelle (syn. *Entosthodon schimperi* Brugués; BRUGUÉS et al. 2001) may complicate the situation. Therefore, it may in part be due to their absence from Hungary that a clear-cut picture was obtained for this country.

It follows that the morphological characters summarised in Table 1 are useful for the distinction of the two species in Hungary. It is possible that the use by earlier workers of other features like costa length, the twisting of the seta, exothecial areolation or peristome ornamentation, features less constant and less reliable, had obscured the concepts of the two species (LOESKE 1929, CRUNDWELL and NYHOLM 1974).

Although the difference in stomatal number between *F. muhlenbergii* and *F. pulchella* had been noted and described in general terms like "frequent" and "less frequent", respectively, by earlier workers (e.g. LIMPRICHT 1895, DE SLOOVER and DEMARET 1968), in this study, for the first time, quantitative data on stomatal number are published. Since the number of stomata per sporophyte does not overlap and the difference in mean value is statistically highly significant, it appears that stomatal number is a discriminating character that can be used profitably in naming plants. Stomatal number in the two species is sufficiently different to allow the use of a less elaborate method for counting stomata than that described in the method section: in fact inspection of one side of an undissected capsule at low magnification (e.g. $\times 40$) may be sufficient.

In a species complex where naming can be critical (CRUNDWELL and NYHOLM 1974), any additional character should be welcome. Therefore, it might be rewarding to examine other taxa of the *F. muhlenbergii* group with respect to stomatal number. Stomatal number as an additional sporophytic character could also be useful for the detection of hybrids.

In other moss genera, e.g. *Ulota*, the taxonomic use of stomatal number may be restricted by a greater amount of variation within taxa, at least partly due to environmental conditions (ERZBERGER, in press). No indication for such variation was found in the present study in Hungarian *Funaria*, but data from wider regions,

more extended field observations and cultivation experiments would be beneficial to obtain a deeper insight into these questions.

Some of the intermediates mentioned by CRUNDWELL and NYHOLM (1974) were attributed to hybridisation between taxa. In the Funariaceae, hybrids have been described both between genera and between species (e.g. MÖNKEMEYER 1927, LOESKE 1929, SMITH 1978, PETTET 1964, ANDREWS 1918, 1942, BRITTON 1895, PODPERA 1954, WETTSTEIN 1932). In Hungary, *F. muhlenbergii* and *F. pulchella* grow in the same places and even form mixed stands, conditions that in principle could favour the formation of hybrids. Apart from these spatial requirements, a temporal condition crucial for hybridisation is the synchronous development of gametes.

According to the results of the phenological analysis, the sporophytes of both species ripen in spring. Although no data are available on the development of gametangia, it seems reasonable to assume that, similarly to sporophyte ripening, formation of gametes and fertilisation also happen at about the same time in both species. In favour of this hypothesis are field observations suggesting that the life cycle of the species in question is completed within a rather short period of time (a few weeks or months).

On the other hand, the collection data of the Hungarian plants suggest that there is on average a difference of about thirteen days in the development of sporophytes between *F. muhlenbergii* and *F. pulchella* (Fig. 6). Field observations on mixed populations of the two species would be needed to establish whether such a difference could in fact operate as an isolating mechanism preventing cross fertilisation.

In the material examined in this study, no evidence for the existence of hybrids was found. It can therefore be concluded that, if hybrids between *F. muhlenbergii* and *F. pulchella* occur in Hungary, they must be quite rare.

Although CRUNDWELL and NYHOLM (1974) showed that the type of *F. mediterranea* Lindb. belongs to *F. muhlenbergii*, according to the description in various handbooks (LOESKE 1929, LIMPRICHT 1895, MÖNKEMEYER 1927) the concept of *F. mediterranea* corresponds to *F. pulchella*. This is characterised (following LIMPRICHT 1895) among others by less serrate leaf margins, finely papillose spores, a shorter theca on a shorter neck, and less frequent stomata. It is therefore astonishing that the specimens labelled *F. mediterranea* form only a minor subset of the specimens revised as *F. pulchella*, and that on the other hand many specimens of *F. muhlenbergii* were labelled *F. mediterranea*, in other words that the coincidence of *F. mediterranea* and *F. pulchella* is as low as that. Boros obviously had tried to get a better understanding of the species complex, as is evident from some revision slips found in specimens of *F. pulchella* with notes like "I var.

meditt.” in his hand or “±átmeneti alak a *F. mediterranea* Lindb.-hez 1929.I.I. Á. Boros”.

The distributional data presented in this study show that *F. muhlenbergii* and *F. pulchella* in Hungary predominantly occur within the same area. They show the characteristic area-type of the sub-Mediterranean element in Hungary (ZÓLYOMI 1942) centring in the Transdanubial uplands, with only few isolated occurrences in the eastern range near Eger and Miskolc, respectively. According to DÜLL (1985), both species show a sub-Mediterranean – suboceanic – montane pattern of distribution. In western and central Europe as well as in Hungary, they occur in lowlands and in the colline region. In Britain *F. muhlenbergii* reaches its highest altitude at 380 m a.s.l. (CRUNDWELL 1994) and in Germany at 370 m a.s.l. (DÜLL 1994), and *F. pulchella* is a lowland plant (CRUNDWELL 1994). However, in the Iberian peninsula, *F. muhlenbergii* occurs at 1,000–1,700 m a.s.l., whereas *F. pulchella* grows at 200–1,450 m a.s.l. (CASAS et al. 1996). *F. muhlenbergii* reaches southern Scandinavia (CRUNDWELL 1994), whereas *F. pulchella* has its most northern records in Scotland (CRUNDWELL 1994) and, on the Continent, in the Odera valley in Germany (ERZBERGER 2002, unpublished; the alleged occurrence in Brandenburg of *F. muhlenbergii* (BENKERT et al. 1995, LUDWIG et al. 1996) erroneously refers to a record of *F. pulchella*).

In Hungary, *F. muhlenbergii* and *F. pulchella* are very similar in geographical distribution. They also occur in the same localities and share the same habitat. Therefore, their ecological demands appear to be very similar. This is best documented by the fact that they can form mixed stands. However, according to the results of the phenological analysis, they may differ in the time of sporophyte ripening.

Although the difference in the mean estimated day of dehiscence is statistically significant, more work is needed to evaluate the biological significance of this result. The time course of sporophyte ripening obviously depends on a number of environmental factors, e.g. the overall meteorological and climatic situation as well as microclimatic and habitat features. The sample of gatherings analysed contains a very large degree of variation in this respect, because specimens were collected at different localities as well as in different years. In the statistical analysis, these differences are in part levelled off, but there remains some uncertainty. Close field observation of mixed stands could perhaps yield some relevant information on the subject, but difficulties are inherent in the varied microhabitats in which the species grow. Thus, when small turfs of plants of *F. pulchella* collected by the author on 21 April 2001 at Pes-kő (Vértestolna) were inspected for the fraction of deoperculate sporophytes, this proportion varied between 0.17 and 0.9 (mean \pm s.d.: 0.53 ± 0.26). On the other hand, cultivation of the two species should not be too difficult, and experiments of that kind might shed light on the question whether

there is an intrinsic difference in the time schedule of sporophyte development. But research of that kind is beyond the scope of the present study.

The habitats of both species in Hungary appear at present not to be threatened by influences of human civilisation. Since, according to the present revision, *F. pulchella* is not less frequent than *F. muhlenbergii*, it cannot be considered an endangered species in Hungary any longer. Besides, *F. pulchella* has been found in five localities recently (PAPP and ERZBERGER 2000, and unpublished collections of the author, see Appendix 1), whereas the latest find of *F. muhlenbergii* dates back to 1966 (Villány Mts, Vajda). Although this may be due to the fact that bryofloristical research intensity has been rather low in Hungary after the period of Boros and Vajda, the possibility cannot be ruled out that the populations of *F. muhlenbergii* have decreased within the last decades. Whether this is so, further field work must show.

* * *

Acknowledgements – I am grateful to the curator of BP, B. Papp, for the loan of specimens, to H. Kürschner for the opportunity to use a Leitz drawing apparatus, to Gy. Szél for help with preparing the maps, to R. McF. Craig for linguistic corrections, and especially to P. Ódor for valuable comments on an earlier version of the manuscript.

REFERENCES

- ANDREWS, A. L. (1918): A new hybrid in Physcomitrium. – *Torreyia* **18**: 52–54.
- ANDREWS, A. L. (1942): Taxonomic notes. II. Another natural hybrid in the Funariaceae. – *Bryologist* **45**: 176–178.
- BENKERT, D., ERZBERGER, P., KLAWITTER, J., LINDER, W., LINKE, CH., SCHAEPE, A., STEINLAND, M. and WIEHLE, W. (1995): Liste der Moose von Brandenburg und Berlin mit Gefährdungsgraden. – *Verh. Bot. Ver. Berlin Brandenburg* **128**(1): 1–68.
- BOROS, Á. (1968): *Bryogeographie und Bryoflora Ungarns*. – Akadémiai Kiadó, Budapest, 466 pp.
- BOROS, Á. and JÁRAI-KOMLÓDI, M. (1975): *An atlas of recent European moss spores*. – Akadémiai Kiadó, Budapest, 466 pp.
- BOROS, Á., JÁRAI-KOMLÓDI, M., TÓTH, Z. and NILSSON, S. (1993): *An atlas of recent European bryophyte spores*. – Scientia Publishing, Budapest, 321 pp.
- BRITTON, E. G. (1895): Contributions to American Bryology, IX. – *Bull. Torrey Botanical Club* **22**: 62–68.
- BRUGUÉS, M., DIRKSE, G. and SÉRGIO, C. (2001): On the taxonomic status and distribution of *Funaria durieui*. – *Cryptogamie, Bryol.* **22**(4): 251–254.
- CASAS, C., BRUGUÉS, M., CROS, R. M. and SÉRGIO, C. (1996): *Cartografía de Briòfits Península Ibèrica i Illes Balears, Canàries, Açores i Madeira* (Bryophyte Cartography Iberian Peninsula, Balearic and Canary Islands, Azores and Madeira). Fasc. IV: 151–200.
- CORLEY, M. F. V. and CRUNDWELL, A. C. (1991): Additions and amendments to the mosses of Europe and the Azores. – *J. Bryol.* **16**: 337–356.

- CORLEY, M. F. V., CRUNDWELL, A. C., DÜLL, R., HILL, M. O. and SMITH, A. J. E. (1981): Mosses of Europe and the Azores; an annotated list of species, with synonyms from the recent literature. – *J. Bryol.* **11**: 609–689.
- CRUNDWELL, A. C. (1994): *Funaria muhlenbergii* Turn., *Funaria pulchella* Philib. – In: HILL, M. O., PRESTON, C. D. and SMITH, A. J. E. (eds): Atlas of the bryophytes of Britain and Ireland. Harley Books, Cardiff, **3**: 26–27.
- CRUNDWELL, A. C. and NYHOLM, E. (1974): *Funaria muhlenbergii* and related European species. – *Lindbergia* **2**: 222–229.
- DE SLOOVER, J.-L. and DEMARET, F. (1968): *Funariaceae*. – In: Ministère de l'agriculture, Jardin botanique national de Belgique. Flore générale de Belgique, Volume III – Fascicule 1. – Jardin Botanique national de Belgique, Bruxelles, 112 pp.
- DÜLL, R. (1985): Distribution of the European and Macaronesian Mosses (Bryophytina) Part II. – *Bryologische Beiträge* **5**: 110–232.
- DÜLL, R. (1994): *Deutschlands Moose* 2. – IDH-Verlag, Bad Münstereifel-Ohlerath, 211 pp.
- ERZBERGER, P. (2002): The number of stomata per sporophyte and its variability in the species of the *Ulota crisa* complex and *Ulota drummondii* (Hook. & Grev.) Brid. (Musc., Orthotrichaceae). – *Lindbergia* [in press]
- GROLLE, R. and LONG, D. G. (2000): An annotated check-list of the Hepaticae and Anthocerotae of Europa and Macaronesia. – *J. Bryol.* **22**: 103–140.
- JÁRAI-KOMLÓDI, M. (1974): Comparative spore morphological examinations in *Funaria* and *Physcomitrium* species. – *Acta bot. hung.* **20**: 71–81.
- LIMPRICHT, K. G. (1895): *Die Laubmoose Deutschlands, Oesterreichs und der Schweiz, Funaria*. – In: Rabenhorst's Kryptogamenflora von Deutschland, Oesterreich und der Schweiz **4**, ed. 2., Leipzig, II: 194–200.
- LOESKE, L. (1929): *Die Laubmoose Europas II. Funariaceae*. – Rep. Spec. Nov. Regn. Veg. Sonderbeihft B, 119 pp.
- LUDWIG, G., DÜLL, R., PHILIPPI, G., AHRENS, M., CASPARI, S., KOPERSKI, M., LÜTT, S., SCHULZ, F. and SCHWAB, G. (1996): Rote Liste der Moose (Anthoceroophyta et Bryophyta) Deutschlands. – *Schriftenreihe für Vegetationskunde* **28**: 189–306.
- MARSTALLER, R. (1993): Synsystematische Übersicht über die Moosgesellschaften Zentraleuropas. – *Herzogia* **9**: 513–541.
- MÖNKEMEYER, W. (1927): *Die Laubmoose Europas*. – In: Rabenhorst's Kryptogamen-Flora, Bd. 4, Leipzig, 956 pp.
- ORBÁN, S. and VAJDA, L. (1983): *Magyarország mohafldrájának kézikönyve*. – Akadémiai Kiadó, Budapest, 518 pp.
- PAPP, B. and ERZBERGER, P. (2000): A Villányi hegység mohafldrája (Bryophyta). – *Dunántúli Dolg. Term. Tud. Sorozat* **10**: 37–45.
- PETTET, A. (1964): Hybrid sporophytes in the Funariaceae I. Hybrid sporophytes on *Physcomitrella patens* (Hedw.) B. & S. and *Physcomitrium sphaericum* (Schkuhr) Brid. in Britain. – *Trans. Brit. bryol. Soc.* **4**: 642–648.
- PODPERA, J. (1954): *Conspectus Muscorum Europaeorum*. – Českoslov. Akademia Ved., Prag, 697 pp.
- RAJCZY, M. (1990): *Mohák – Bryophyta*. – In: RAKONCZAI, Z. (ed.): Vörös könyv. Akadémiai Kiadó, Budapest, pp. 322–325.
- SMITH, A. J. E. (1978): *The moss flora of Britain and Ireland*. – Cambridge University Press, Cambridge, New York, Port Chester, Melbourne, Sidney, 706 pp.
- WETTSTEIN, F. von (1932): *Genetik*. – In: VERDOORN, F. (ed.): Manual of Bryology. Nijhoff, The Hague, pp. 233–272.

ZÓLYOMI, B. (1942): A közép-dunai flóraválasztó és a dolomitjelenség. (Die Mitteldonau-Florenscheide und das Dolomitphänomen). – *Bot. Közlem.* 39: 209–231.

(Received: 25 March, 2002)

Appendix 1. List of specimens [additions of the author are in square brackets]

Funaria muhlenbergii

Bükk Mts – BP 114931: Comit. Borsod. In rupibus calcareis montis Várhegy prope Görömböly-Tapolca, ca. 200 m.s.m. leg. Boros 22.5.1937.

Pilis Mts – BP 6798, BP 114934: Comit. Esztergom. In rupestribus calcar. sept. montis Háromszáz-garádics prope Pilisszentlélek, 550 m.s.m. leg. Boros 28.4.1946. [The specimen BP 114934 is the voucher specimen of the spore micrographs of *Funaria dentata* in JÁRAI-KOMLÓDI (1974), *Funaria muhlenbergii* in BOROS and JÁRAI-KOMLÓDI (1975) and BOROS et al. (1993)]. – BP 6800: Com. Esztergom. In rupibus calcareis montis Öregszirt, Kétáguhegy supra pag. Kesztölc leg. L. Vajda 28.4.1946.

Buda Mts – BP 63862: Comit. Pest. In rupibus dolomitibus montis Kis Szénás supra pag. Pilisszentiván leg. L. Vajda 18.4.1960. – BP 114920: Comit. Pest. In humosis inter saxa calc. umbr. vallis ad pedem merid. montis Remetehegy pr. Máriaremete, alt. ca. 300 m.s.m. leg. Boros 20.6.1923. – BP 114922: Comit. Pest. In calcareis montis Remete-hegy ad Máriaremete, alt. ca. 3–400 m.s.m. leg. Boros 28.3.1926. – BP 114924: Comit. Pest. In humosis inter saxa calc. merid. montis Remetehegy pr. Máriaremete, alt. ca. 3–400 m.s.m. leg. Boros 20.5.1945.

Gerecse Mts – BP 114907: Comit. Komárom. In rupestribus calcareis montis Tardosi Gorba prope Tardos, alt. ca. 400 m.s.m. leg. Boros 7.5.1933. – BP 114906: Comit. Komárom. In rupestribus calc. or. montis Halyagoshegy prope Vértestolna, alt. ca. 400 m.s.m. leg. Boros 26.4.1931. – BP 6808: Hung. occid. Montes Gerecse: in mte "Peskő" pr. pag. Alsógalla, in terra humosa calc., alt. cca. 500 m leg. Szepesfalvy 2.6.1935. – BP 114903: Comit. Komárom. In humosis inter saxa calc. montis Peskő prope Tarján, alt. ca. 350–400 m.s.m. leg. Boros 2.6.1935. – BP 114905: Comit. Komárom. In calcareis montis Peskő prope Tarján, alt. ca. 3–400 m.s.m. leg. Boros 29.4.1928. – BP 114900: Comit. Komárom. In humosis inter saxa dolomit. montis Bagoly-hegy prope pag. Gyermely, alt. ca. 250 m.s.m. leg. Boros 22.5.1941. – BP 114899: Comit. Komárom. In rupibus calcar. merid. montis Veres-hegy prope pagum Alsógalla [Tatabánya, Vörös-hegy], alt. ca. 300 m.s.m. leg. Boros 2.4.1939.

Vértes Mts – BP 114908: Comit. Komárom. In humosis inter saxa calc. partis sept. montis Suhogó pr. Vértesomló, alt. ca. 300 m.s.m. leg. Boros 14.4.1935 [A duplicate in S-PA of this gathering is quoted by CRUNDWELL and NYHOLM (1974)]. – BP 6801, BP 114911: Comit. Komárom. In rupibus calcar. occid. dumet. montis Lófő supra pag. Várgesztes, alt. ca. 350 m.s.m. leg. Boros 29.4.1935. – BP 114890: Comit. Fejér. In rupibus dolomitibus vallis Tamás-árok prope pag. Szár, leg. Dr. Z. Zsák 22.6.1940. – BP 114882, BP 114883: Comit. Fejér. In rupibus dolomit. ad "Macskagödör" vallis "Fánien-völgy" prope Vérteskozma, alt. ca. 300 m.s.m. leg. Boros 1.5.1932. – BP 6807, BP 114888: Comit. Fejér. In rupestribus dolomitibus vallis Csatorna-völgy prope Csákberény, alt. ca. 3–350 m.s.m. leg. Boros 20.6.1935 [A duplicate in S-PA of this gathering is quoted by CRUNDWELL and NYHOLM (1974)]. – BP 114889: Comit. Fejér. In humosis inter saxa dolomit. in rupestribus vallis Csatorna-völgy prope Csákberény, alt. ca. 3–400 m.s.m. leg. Boros 17.4.1949 [mixed gathering with

F. pulchella, containing a piece of substrate with a mixed stand]. – BP 6806, BP 114887: Comit. Fejér. In rupibus dolom. umbrosis montis Kistábor-hegy prope Csákvár, alt. ca. 350 m.s.m. leg. Boros 7.4.1935.

Bakony Mts – BP 89872: Com. Veszprém, prope Csesznek, Czuhatatak völgye. In decliv. mont. meridon. Solo calcareo, ca. 370 m leg. Péntes 6.6.1928. – BP 114928: Comit. Veszprém. In humosis inter saxa calc. vallis Cuhavölgy pr. Csesznek, alt. ca. 400 m.s.m. leg. Boros 7.6.1928. – BP 27044: Comit. Veszprém. In rupibus calcareis Forrasztókö montis Somberek hegy prope pag. Ugod, montes Bakony, leg. L. Vajda 5.4.1954; BP 114927: Comit. Veszprém. In rupestribus calcar. montis Somberek "Forrasztókö" dict. prope Ugod, alt. ca. 3–350 m.s.m. leg. Boros 5.4.1954. – BP 114925: Comit. Fejér. In humosis inter saxa dolomit. montis Baglyas-hegy pr. Inota, alt. ca. 2–300 m.s.m. leg. Boros 6.4.1951. – BP70981: Comit. Veszprém. In rupibus dolomitibus siccis vallis rivi Sédpatak prope pag. Veszprém; mtes. Bakony leg. L. Vajda 20.6.1965; BP 114930: Comit. Veszprém. In rupestribus dolomit. vallis rivi Séd prope Veszprém, alt. ca. 250 m.s.m. leg. Boros 20.6.1965. – BP 62490: Comit. Veszprém. In monte Csobánc [Diszel] leg. L. Vajda 1.5.1959. – BP 57033: Comit. Veszprém. In rupibus calcareis montis Kispúposhegy prope pag. Zalasántó leg. L. Vajda 1.5.1956. – BP 114913: Comit. Zala. In humosis inter saxa dolomit. montis Pupos-hegy prope Rezi, alt. ca. 300 m.s.m. leg. [Boros' wife ("legit uxor mea")] 1.5.1956. – BP 49010: Comit. Veszprém. In rupibus calcareis montis Kümell prope pag. Rezi leg. L. Vajda 1.5.1956. – BP 26284: Comit. Veszprém. In rupibus calcareis in sylvestribus vallis Horogvölgy prope pag. Akali leg. L. Vajda 17.4.1953.

Mecsek Mts – BP 114915, BP 114916: Pécs, a Szt. Bertalan-hegy nagy szikláit alatt. Mészkö Triaskalk sonnig trocken, kb. 380 m. tszf. leg. Dr. Visnya Aladár 18.7.1934.

Villány Mts – BP 70983: Hungaria merid. Comit. Baranya. In rupestribus montis Tenkes, prope pag. Máriagyűd leg. L. Vajda 26.3.1965. – BP 71518: Comit. Baranya. In graminosis montis Szársomlyó, montes Villányi hegység leg. L. Vajda 7.3.1966. – BP 71519: Comit. Baranya. In rupestribus montis Szársomlyó, montes Villányi hegység leg. L. Vajda 7.3.1966. – BP 114917: Comit. Baranya. In calcareis montis Harsányi-hegy ad Nagyarsány, alt. ca. 2–400 m.s.m. leg. Boros 16.5.1926. – BP 114919: Comit. Baranya. In humosis inter saxa calcar. merid. montis Harsány-hegy prope Nagyarsány, alt. ca. 3–400 m.s.m. leg. Boros 27.4.1952.

Funaria pulchella

Bükk Mts – BP 6811: Com. Heves. In rupestribus montis Bervahegy prope pag. Felnémet [Eger] leg. L. Vajda 22.4.1951. – BP 114932: Comit. Heves. In rupestribus calcar. occ. supra vallem Berva-völgy prope Felnémet, alt. ca. 300 m.s.m. leg. Boros 22.4.1951.

Danube valley – BP 47074: Comit. Pest. In declivibus arenosis prope pag. Alsógöd leg. L. Vajda 15.4.1956; BP 89253, BP 114918, BP 162946: Com. Pest. In arenosis ad viam ferream versus Alsógöd prope Dunakeszi, alt. ca. 130 m.s.m. leg. Boros 15.4.1956; BP 114914: Comit. Pest. In arenosis ad viam ferream prope Dunakeszi, versus Alsógöd, alt. ca. 133 m.s.m. leg. Boros 24.4.1951. [A duplicate in GL of this gathering is quoted by CRUNDWELL and NYHOLM (1974); the specimens from Alsógöd in BP have been revised by M. Rajczy as *F. pulchella* in 1984].

Pilis Mts – Erzberger 7042, 7044: Comit. Komárom-Esztergom, Dorog, Strázsa-hegy, offener Kalkfelsrasen, leg. et det. P. Erzberger 26.4.2001. – BP 114933: Comit. Pest. In humosis inter saxa calc. montis Csucs-hegy prope pag. Csobánka, alt. ca. 3–350 m.s.m. leg. Boros 30.3.1947.

Buda Mts – BP 68504: Comit. Pest. In rupestribus montis Nagyszénás prope pag. Nagykovácsi leg. L. Vajda 5.3.1961. – Erzberger 6939: Comit. Pest, Telki, Fekete-hegyek, Sziklafal, auf Erde über Kalkgestein leg. et det. P. Erzberger 18.4.2001. – BP 114921: Comit. Pest. In humosis inter saxa calc. merid. montis Remetehegy pr. Máriaremete, alt. ca. 300 m.s.m. leg. Boros 20.6.1923; BP 6795, BP

6797, BP 119423: Comit. Pest. In rupestribus montis Remetehegy ad Mária-Remete leg. Degen 28.3.1926. – BP 114939: Budapest. In rupibus apricis dolomitibus montis Guggerhegy, alt. ca. 300 m.s.m. leg. Boros 9.4.1928. – BP 114938: Budapest. In rupibus apricis dolomitibus montis Kecshegy, alt. ca. 300 m.s.m. leg. Boros 9.4.1928; BP 114940: In humosis inter saxa dolomit. montis Kecshegy prope Budapest, alt. ca. 350 m.s.m. leg. Boros 25.3.1926. – BP 6793, BP 114942: Budapest. In humosis inter saxa dolomit. montis Kiskecshegy, alt. ca. 350 m.s.m. leg. Boros 30.3.1934; BP 114941: In humosis inter saxa dolom. montis Kiskecshegy prope Budapest, alt. ca. 350 m.s.m. leg. Boros 24.3.1935. – BP 114935: Budapest. In dolomitibus apricis vallis Farkas-völgy, alt. ca. 300 m.s.m. leg. Boros 6.5.1945. – BP 89871, BP 114937: prope oppid. Budapest Farkasrét In decliv. meridion. calcareo ca. 300 m leg. Dr. Péntes A. 10.4.1947. – BP 114936: Budapest. In dolomitibus montis Sas-hegy, alt. ca. 2–250 m.s.m. leg. Boros 6.5.1945.

Gerecse Mts – BP 6799, BP 114904: Comit. Esztergom. In humosis inter saxa calcar. mer.-or. montis Nagyteke-hegy prope pag. Süttő, alt. ca. 2–300 m.s.m. leg. Boros 17.5.1941. – BP 6796, BP 114902: Comit. Esztergom. In humosis inter saxa calcarea montis Öregkő prope Bajót, alt. ca. 3–375 m.s.m. leg. Boros 5.4.1936. – Erzberger 6992, 7001: Comit. Komárom-Esztergom, Vértestolna, Puskó, auf dünner Erdschicht über Kalkplatten leg. et det. P. Erzberger 21.4.2001. – BP 114901: Comit. Komárom. In humosis inter saxa dolomit. merid. montis Kecskő prope pagum Gyermely, alt. ca. 250 m.s.m. leg. Boros 25.3.1941. – BP 114894: Comit. Komárom. In humosis inter saxa calc. ad monum. "Turul" supra Bánhida, alt. ca. 300 m.s.m. leg. Boros 2.4.1939; BP 114895, BP 114896: Comit. Komárom. In humosis inter saxa calc. ad monum. "Turul" in monte Kő-hegy prope Bánhida, alt. ca. 300 m.s.m. leg. Boros 1.5.1938. – BP 114897: Comit. Komárom. In rupibus calcar. merid. montis Veres-hegy prope Alsógalla [Tatabánya, Vörös-hegy], alt. ca. 300 m.s.m. leg. Boros 25.4.1948; BP 114898: Comit. Komárom. In rupibus calcar. merid. montis Veres-hegy prope Alsógalla [Tatabánya, Vörös-hegy], alt. ca. 330 m.s.m. leg. Boros 26.4.1931. – BP 6804, BP 114881: Comit. Fejér. In humosis inter saxa dolomit. montis Lóingató-hegy prope pagum Óbarok, alt. ca. 250 m.s.m. leg. Boros 7.4.1940.

Vértes Mts – BP 114912: Comit. Komárom. In humosis inter saxa calc. montis Gadóz supra pag. Várgesztes, alt. ca. 350 m.s.m. leg. Boros 29.4.1935. – BP 6802, BP 114910: Comit. Komárom. In humosis inter saxa calc. apricis montis Lőfő supra pag. Várgesztes, alt. ca. 350 m.s.m. leg. Boros 29.4.1935. – BP 114909: Comit. Komárom. In humosis inter saxa calc. montis "464" supra Kapberek-pusztá prope Vértessomló, alt. ca. 4–450 m.s.m. leg. Boros 19.5.1935. – BP 114893: Comit. Fejér. In humosis inter saxa dolomitica montis Zuppa prope pagum Szár, alt. ca. 300 m.s.m. leg. Boros 14.5.1942. – BP 114891: Comit. Fejér. In rupibus dolomit. montis Boglári-hegy prope Vérteskozma, alt. ca. 350 m.s.m. leg. Boros 25.3.1935; BP 114892: Comit. Fejér. In humosis inter saxa dolom. montis Kissomló-hegy prope Vérteskozma, alt. ca. 380 m.s.m. leg. Boros 7.4.1935. – BP 6803, BP 114886: Comit. Fejér. In collibus siccis dolomit. ad Kőlik-hegy prope Csákberény, alt. ca. 2–230 m.s.m. leg. Boros 17.5.1937. – BP 114885: Comit. Fehér. In humosis inter saxa calcar. supra Csókakő, alt. ca. 3–400 m.s.m. leg. Boros 3.4.1927. – Erzberger 7015: Comit. Fejér, Csókakő, offener Dolomitfelsrasen nördl. Burgruine leg. et det. P. Erzberger 23.4.2001. – BP 114889: Comit. Fejér. In humosis inter saxa dolomit. in rupestribus vallis Csatorna-völgy prope Csákberény, alt. ca. 3–400 m.s.m. leg. Boros 17.4.1949 [mixed gathering with *F. muhlenbergii*, containing a piece of substrate with a mixed stand]. – BP 114880: Comit. Fejér. In rupestribus dolomit. sept. silvat. adversus montem Ökörállás prope Csákvár, alt. ca. 250 m.s.m. leg. Boros 18.5.1962. – BP 6805, BP 114884: Comit. Fejér. In humosis inter saxa dolom. montis Szőlő-kő prope Csákvár, alt. ca. 2–240 m.s.m. leg. Boros 21.3.1937.

Bakony Mts – BP 26940: Comit. Fejér. In rupestribus calcareis cacuminis montis Baglyashegy prope Csór leg. L. Vajda 28.3.1954; BP 114926: Comit. Fejér. In humosis inter saxa dolomit. montis

Baglyas-hegy prope Csór, alt. ca. 2–350 m.s.m. leg. Boros 28.3.1954; BP 114929; Comit. Fejér. In rupestribus dolomitibus montis Baglyas-hegy prope Inota, alt. ca. 2–300 m.s.m. leg. Boros 15.5.1955.

Villány Mts – BP 166720; Comit. Baranya. In abrupte loessacea Macskalyuk in decl. merid. montis prope pag. Máriagyúd, alt. ca. 200–250 m.s.m. leg. B. Papp 8.8.1999 (PAPP and ERZBERGER 2000).

Appendix 2. Evaluation of collection dates with respect to the phenology of sporophyte ripening

In order to take account of the fact that specimens contain sporophytes in different stages of development, an attempt was made to estimate an approximate "day of dehiscence", i.e. the day when just 50% of the sporophytes are deoperculate. This day would be earlier than the date of collection, if the specimen contained mostly deoperculate sporophytes, but it would be later in case of unripe sporophytes. The corrections applied in this study are less than 7 days in all cases and were computed in the following way.

First, the fraction of deoperculate sporophytes f was estimated in each specimen. f was then used to compute the "estimated day of dehiscence" d from the date of collection c (both counted in days from the beginning of March), using the following relationship: $d = c + r(0.5 - f)$, where r is the range of the correction.

In the present analysis, $r = 13$. Taking into consideration that in most populations development of sporophytes is not very synchronous, but shows rather great variation among individual plants, the value of 13 for the estimated range r of the correction appears rather low. Using higher values for r (e.g. 30 or 60) does not essentially alter the conclusions of the analysis.

It has often been observed that sporophytes continue ripening after collection. Therefore, the phenological stage observed in a specimen need not be identical with the stage at the time of collection, but might show a higher percentage of deoperculate sporophytes. To examine the possible influence of post-collection ripening on the results, the mean value of f was calculated for the two species: In *F. muhlenbergii* $f = 0.4606 \pm 0.06676$, in *F. pulchella* $f = 0.4711 \pm 0.05532$ (mean \pm s.e.). In both cases f is not significantly different from 0.5 (t-test). If post-collection ripening was strong, the mean value for f would be expected to be higher than 0.5, provided the sample of specimens is not biased in favour of unripe sporophytes. However, there is no reason to assume that kind of bias; on the contrary, collectors would tend to pick up plants with rather ripe sporophytes if there is a choice.

In principle, post-collection ripening might be different in the two species, especially since they differ in theca size. In a given specimen, post-collection ripening would result in a higher value of f and thus in a lower value of d , depending on the magnitude of the range r of the correction. However, the observed difference in sporophyte ripening of about 12–13 days is independent of the value of r and is also obtained for the uncorrected collection dates. It was therefore concluded that post-collection ripening of sporophytes did not influence the results.