

*DITRICHUM CRISPATISSIMUM* (MUELL. HAL.) PARIS, A NEW  
SPECIES OF THE HUNGARIAN BRYOFLORA, AND  
*DITRICHUM FLEXICAULE* (SCHLEICH. EX SCHWAEGR.)  
HAMPE IN HUNGARY

P. ERZBERGER

*Belziger Str. 37, D-10823 Berlin, Germany*

During the revision of 181 herbarium specimens of *Ditrichum flexicaule* s. l. from BP a single tuft of *Ditrichum crispatisimum* was found in a specimen that had been collected in 1963 by L. Vajda at Koloska rocks, north of Lake Balaton. The features of these Hungarian plants and the character states separating *D. crispatisimum* from *D. flexicaule* s. str. are described in detail. Among the specimens of *D. flexicaule* s. str. some have character states approaching *D. crispatisimum*. Aspects of the taxonomy of the *D. flexicaule* complex are discussed.

Key words: *Ditrichum crispatisimum*, *Ditrichum flexicaule*, distribution, Hungary, map, diagnostic characters

## INTRODUCTION

In a taxonomic and nomenclatural study of the variable and heterogeneous *Ditrichum flexicaule* complex, FRISVOLL (1985) presented the concept of two distinct taxa treated by him as species, *D. flexicaule* s. str. and *D. crispatisimum*. (From this point onwards, *D. flexicaule* always means *D. flexicaule* s. str. unless stated otherwise.)

His concept was obviously accepted by several authors who enumerated *D. crispatisimum* and *D. flexicaule* as separate species in checklists, e.g. CORLEY and CRUNDWELL (1991), CASAS (1991), SÉRGIO *et al.* (1994), LUDWIG *et al.* (1996), WERNER (1999), or studied the distribution of Frisvoll's taxa in certain regions of Europe, e.g. the Iberian peninsula (CASAS *et al.* 1990, 1992), the British Isles (SMITH 1993) and the Czech and Slovak Republics (NOVOTNÝ 1997). From these studies it appeared that the segregate *D. crispatisimum* is widespread and frequent in western Europe, but becomes rarer towards the east, while *D. flexicaule* is e.g. rare in Britain, but frequent in more continental parts of central Europe. In the Iberian peninsula, the two species occupy areas that overlap in the northeast, otherwise *D. crispatisimum* is nearly completely restricted to a zone along the south coast of the Bay of Biscay in northern Spain, whereas *D. flexicaule* extends far south along a zone parallel to the western coast of the Mediterranean. This distributional pattern is interpreted as reflecting different ecological needs of the two species: *D. crispatisimum* requires more and more constant humidity, *D. flexi-*

*caule* is more drought-resistant (CASAS *et al.* 1990). This is in agreement with an Atlantic affinity in *D. crispatisimum* and a more continental character in *D. flexicaule*.

But acceptance of Frisvoll's concept is not unanimous. NOVOTNÝ (1997), using morphometrical and multivariate methods, claims the existence of transitional forms together with Frisvoll's taxa in former Czechoslovakia. Intermediate forms are also mentioned by SAUER (2000) for Southwest Germany.

In Hungary, *D. flexicaule* s. l. is frequent (BOROS 1968, ORBÁN and VAJDA 1983). Its distribution in Hungary and the surrounding Carpathian region has been compiled by ORBÁN (1974), but has not yet been treated taxonomically. For the preparation of an updated checklist of Hungarian bryophytes the following interrelated questions had to be answered:

- Does *D. crispatisimum* occur in Hungary?
- Can Frisvoll's concept successfully be applied to describe the variation within *D. flexicaule* s. l. in Hungary, or is the resolution of the complex complicated in continental Europe by intermediates as suggested by NOVOTNÝ (1997)?

As a contribution towards answering these questions, the specimens labelled *D. flexicaule* in BP collected in Hungary were revised. The results are presented in this paper.

## MATERIAL AND METHODS

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

Abbreviations of the herbariums: BP = Hungarian Natural History Museum, Budapest; B = Botanischer Garten und Botanisches Museum, Berlin-Dahlem.

### Taxonomic characters separating *Ditrichum crispatisimum* and *D. flexicaule*

Initially, difficulties were encountered with the correct interpretation of some character states described in the literature for the differentiation between *D. crispatisimum* and *D. flexicaule*. Therefore, in addition to the 181 Hungarian specimens from BP some specimens from the author's herbarium and from B were studied. With the use of FRISVOLL (1985), among these additional specimens, six could be identified as *D. crispatisimum*. They originate from different parts of western and central Europe (Ireland, Scotland, France, Italy, Germany), and show the character states typical of this taxon. It turned out that some comments on the

character states differentiating between *D. crispatisimum* and *D. flexicaule* published after the detailed and well illustrated study of FRISVOLL (1985) are rather misleading (see Discussion).

The following account is based essentially on FRISVOLL (1985), but since that paper might not be easily accessible, the main features are summarized in Table 1 and commented below (slight modifications based on observations of the author are included).

**Habit** is very variable in both species. At one extreme there is *D. flexicaule* with very low, compact turfs (this morph is often called var. *densum* (B., S. et G.) Braithw.), and at the other we find tall lax cushions, which is the usual habit of *D. crispatisimum*. However, stunted forms of *D. crispatisimum* may have the ap-

**Table 1.** Character states of *Ditrichum crispatisimum* and *D. flexicaule* (after FRISVOLL (1985), modified).

| Character                                                            | <i>D. crispatisimum</i>                                       | <i>D. flexicaule</i>                                                      |
|----------------------------------------------------------------------|---------------------------------------------------------------|---------------------------------------------------------------------------|
| Habit                                                                | in lax tufts, strongly tomentose                              | in dense tufts, usually less tomentose                                    |
| Height                                                               | > 4 cm                                                        | < 5 cm                                                                    |
| Flagellae                                                            | common                                                        | absent (except in arctic material)                                        |
| Orientation of dry leaves                                            | straight                                                      | flexuose                                                                  |
| Leaf length                                                          | > 3.5 mm                                                      | < 3 mm                                                                    |
| Leaf shape                                                           | sheathing base gradually tapering towards subula              | sheathing base abruptly narrowed into subula                              |
| Subula length                                                        | > 2/3 of total leaf length                                    | < 2/3 of total leaf length                                                |
| Leaf apex                                                            | often denticulate far down the subula                         | entire except a few denticulations at extreme apex                        |
| Cells (in the middle) of the sheathing part of the leaf              | elongate with curved walls                                    | isodiametric with straight walls                                          |
| Basal cells near costa                                               | long, porose                                                  | short, eporose                                                            |
| Marginal cells                                                       | thin-walled, forming broad hyaline border merging into lamina | thick-walled, forming narrow hyaline border distinct from adjacent lamina |
| Dorsal costa cells (in the middle of the sheathing part of the leaf) | shorter than adjacent lamina cells                            | longer than adjacent lamina cells                                         |
| Auricles                                                             | absent                                                        | often present                                                             |
| (Innermost) perichaetial leaves                                      | suddenly narrowed into subula                                 | gradually narrowed into subula                                            |

pearance of *D. flexicaule*, and lax, long forms of *D. flexicaule* exist (e.g. the Hungarian specimens from Sas-kő in Mátra Mts). Tomentum may be strong in *D. crispatisimum* and weak in *D. flexicaule*.

In the original material studied by FRISVOLL (1985), **stem length** is (1–) 4–5 (–9) cm in *D. crispatisimum* and (1.5–) 4–5 (–7) cm in *D. flexicaule*, i.e. considerable overlap exists.

Short-leaved **flagelliferous shoots** are absent from *D. crispatisimum*, but fragile branches with unmodified leaves occur.

**Orientation of dry leaves** is a very characteristic feature of the taxa that is easily recognized even at low magnifications. In contrast with the meaning of the specific epithet “*crispatisimum*” the leaves of *D. crispatisimum* are rather straight, usually slightly or not at all flexuose (except in some sheltered habitats), often falcate; those of *D. flexicaule* are usually flexuose, rarely falcate. The long subulae of *D. crispatisimum* are, however, often spirally twisted together, which happens only rarely in *D. flexicaule* with its generally shorter subulae.

**Leaf length** is related to robustness, thus leaves of *D. crispatisimum* are 4–5 (–7.2) mm long, while those of *D. flexicaule* are (1.4–) 3 (–4.6) mm long, but this character is very strongly dependent on growth conditions, dry-growing ecads having much shorter leaves in both taxa. In mixed stands, however, *D. crispatisimum* always has longer leaves than *D. flexicaule*.

**Leaf shape** and **subula length** are interrelated. Leaves of *D. crispatisimum* are gradually narrowed from a convolute expanded part into a subula that makes up more than 2/3 of total leaf length, whereas in *D. flexicaule* the sheathing leaf base is rather suddenly contracted into a comparatively short subula. This character is not always easy to establish, because some leaves may appear intermediate. The upper limit of the sheathing leaf base may be difficult to assess in leaves that gradually taper towards the subula, in which case the relative length of the subula is hard to estimate. In contrast with *D. flexicaule*, in typical *D. crispatisimum* the leaf is not really sheathing the stem. The difference in leaf insertion is well illustrated in CASAS *et al.* (1990). It is important that vegetative leaves are examined, because perichaetial leaves have a different form (and also areolation).

Dentation of the **leaf apex** is variable in both taxa and thus seems to be of less value in naming plants.

**Cells (in the middle) of the sheathing part of the leaf** are variable in both taxa but usually shorter in *D. flexicaule*. Cell length is not constant within a leaf, but varies in a gradient, cells becoming shorter towards the apex. At the top of the sheathing part, lamina cells may be isodiametric in both taxa, therefore this character must be studied further down. Plants of both taxa growing in dry places have shorter lamina cells. Some cells of the upper part of the sheathing base in *D.*

*crispatissimum* usually have curved walls, while cell walls in *D. flexicaule* are usually straight or only slightly curved.

**Basal juxtacostal cells** in *D. crispatissimum* are usually narrowly elongate and distinctly porose, at least in some leaves (several leaves have to be studied!), whereas in *D. flexicaule* the cells are slightly shorter and usually eporose, sometimes indistinctly porose. This and the preceding character are stressed by Frisvoll of being of particular importance in naming plants.

**Marginal cells** form some kind of hyaline border around the middle of the sheathing leaf part in both taxa, but these cells are longer, more thin-walled in *D. crispatissimum*, the border is (1)2–4 cell rows broad and indistinctly delimited towards the inner cells, whereas in *D. flexicaule* cells are shorter, have thicker walls, and the border is (0)1–2(3) rows broad and usually distinctly marked towards the inner cells.

Considerable difficulty was encountered with the observation of **dorsal costa cells** in relation to adjacent lamina cells. A detailed investigation of some typical specimens of both taxa revealed that two additional circumstances have to be taken into account:

(i) Length of costa cells as well as that of lamina cells varies in a gradient from leaf base to apex. Dorsal costa cells are longest at the leaf base, becoming progressively shorter towards the upper end of the sheathing leaf base, then remain constant or slightly increase in length towards the apex. Lamina cells show a similar trend, but to a different extent, depending on the species and also on habitat conditions; dry-growing ecads having shorter cells.

(ii) Dorsal costa cells are not homogeneous, but rows of shorter cells often alternate with rows of longer cells, these rows sometimes extending over a few cells only. This feature is evident in Frisvoll's illustrations (Figs 1 and especially 15), but its relevance is not considered by that author.

When comparing the length of dorsal costa cells and lamina cells, it must therefore be specified (i) which part of the leaf is examined and (ii) if short or long costa cells (or average values) are considered.

In the author's experience, a comparison of dorsal costa cells and adjacent lamina cells should be made at or slightly above the middle of the sheathing part of the leaf. At this point of the cell length gradients, in *D. crispatissimum* lamina cells are still rather long and costa cells have already shortened to the extent that longer lamina cells are adjacent to short costa cells (Fig. 15 in FRISVOLL 1985), whereas in *D. flexicaule* lamina cells are in general shorter and dorsal costa cells longer, so that anywhere from leaf base to apex lamina cells will be found to be shorter than costa cells.

Due to the fact that dorsal costa cells are not uniform in length even at a given point of the cell length gradient, several cells must be considered in an effort to obtain a representative average value. It is not correct to compare the longest costa cells to the shortest lamina cells, because that would result in costa cells appearing longer than lamina cells even in *D. crispatisimum*, as can be seen also on Figure 15 in FRISVOLL (1985); the converse procedure – comparing the shortest costa cells with the longest lamina cells – must also be rejected, since it might in some cases attribute the character state of *D. crispatisimum* to *D. flexicaule*. Comparing the shortest cells of costa and lamina respectively with each other, however, appears to give correct results in the majority of cases, as well as comparing the longest cells.

The difficulties encountered in this feature are further aggravated by the variability due to growth conditions and geographical region, as FRISVOLL (1985) points out. SMITH (1993) rejects this character as too variable to be of use.

In *D. crispatisimum*, **auricles** are absent, whereas in *D. flexicaule* they are frequently present, although this may vary within leaves of the same stem.

**Perichaetial leaves** encircling a fully grown seta must be studied. It is essential to examine the innermost 1–2 leaves, because in *D. flexicaule* some outer leaves can have a sheathing leaf base that is rather abruptly narrowed into the subula. Therefore it is better not to dissect the perichaetium but to observe the leaves *in situ*. In fertile specimens this appears to be a very valuable character.

## RESULTS

Among the 181 specimens from BP examined, one was found to contain typical *D. crispatisimum*, 178 specimens were referred to *D. flexicaule* s. str., and two belonged to genera other than *Ditrichum* (*Dicranum*, *Dicranella*). A few specimens of *D. flexicaule* showed to a various degree certain of the features ascribed to *D. crispatisimum* by FRISVOLL (1985). These might thus be interpreted as intermediates.

### *Ditrichum crispatisimum* and *D. flexicaule* at Koloska rocks in Hungary

A single tuft of *D. crispatisimum* was found together with several tufts of *D. flexicaule* s. str. in a specimen collected by L. Vajda in 1963 in the hills north of Lake Balaton (Fig. 1): BP 68224, Herbarium Musei Hist. Nat. Hung., Budapest, Flora Hungarica, *Ditrichum flexicaule* (Schleich.) Hampe cum *Scapania calcicola*. Comit. Veszprém. In rupibus dolomitcis Koloska sziklák supra vall. Koloska-

völgy prope pag. Balatonfüred 20.V.1963 L. Vajda. rev. P. Erzberger as *D. crispatissimum*, t. C. Casas.

The following description is based on this Hungarian specimen (only characters of relevance for the distinction between Frisvoll's taxa are mentioned).

Plants robust, of yellowish colour, the basal parts brown, stem length 5–6 cm, in loose tuft, very sparsely tomentose at basal parts of stems only, short-leaved flagelliform shoots not seen. Dry leaves very slightly flexuose, some slightly falcate, subulae at stem apex sometimes spirally twisted together. Vegetative leaves 3–3.8 mm long, gradually narrowed into subula, which makes up more than 2/3 of leaf length, subula entire except a few denticulations at extreme apex only; costa slightly convex dorsally, ill-defined, dorsal cells of costa at the middle of the sheathing leaf base in some leaves more elongate than adjacent lamina cells, in some leaves of comparable size or shorter; subula bistratose in upper part, in lower part laminal wings unistratose with unistratose marginal border; cells in upper part of sheathing leaf base on average 15(–18)  $\mu\text{m}$  long, in middle part of sheathing leaf base more variable, (10–) 13–22 (–25)  $\mu\text{m}$  long, elongate with curved walls, cells in lower part of sheathing leaf base towards costa (37–) 44 (–53)  $\mu\text{m}$  long, elongate and porose, in some leaves shorter, ca 30  $\mu\text{m}$  long, and only slightly porose; cells of marginal border narrow, elongate, more or less hyaline, grading without clear limitation into lamina cells; auricles not seen. Perichaetial leaves not seen.

The plants closely follow the description of *D. crispatissimum* by FRISVOLL (1985). Some character states do not show the expression typical of *D. crista-*

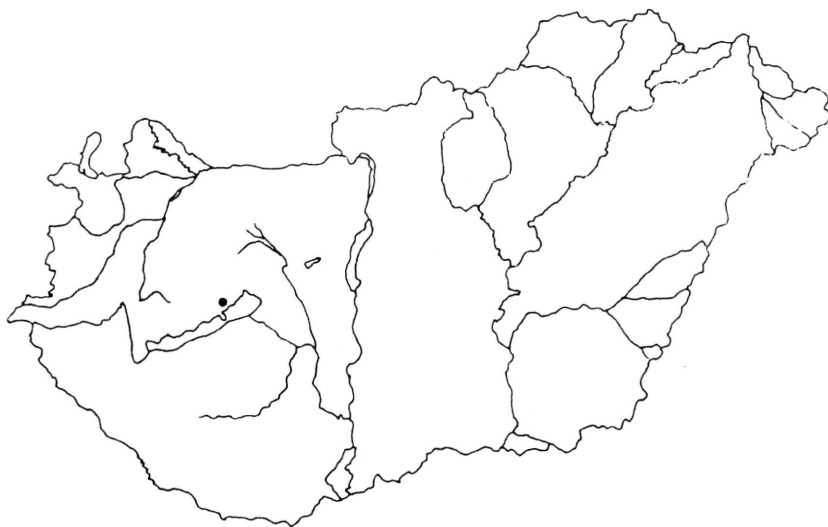


Fig. 1. Record of *Ditrichum crispatissimum* in Hungary.

*tissimum*, but are still within the range of variability as indicated in FRISVOLL (1985), e.g. leaf length is rather short in the Hungarian specimen, but still at the lower limit for *D. crispatisimum* (see Table 1 in FRISVOLL 1985): a leaf length of 3.1–4.6 mm is given for *D. fragilicuspis* Dix. et Sainsb., a synonym of *D. crispatisimum*; the apical part of the subula is said to be frequently denticulate in *D. crispatisimum*, but sometimes almost entire; dorsal cells of the costa are usually shorter than adjacent lamina cells in *D. crispatisimum*, although FRISVOLL (1985) reports them to be sometimes more elongate in northern areas. C. Casas, who kindly examined part of the specimen, confirmed the correctness of the determination.

A duplicate gathering (BP 68111) did not contain *D. crispatisimum*, only *D. flexicaule* s. str. However, these plants, as well as those included with the tuft of *D. crispatisimum* in BP 68244, were not typical *D. flexicaule* s. str., but showed certain character states of *D. crispatisimum*. They differ from the tuft of *D. crispatisimum* in the following respects.

Plants of different appearance, less robust, of yellowish green colour, stem length 3–3.5 cm, in moderately dense tufts, matted with a moderate amount of tomentum except for the most recent apical growth, which is free of tomentum; short-leaved flagelliform shoots present. Dry leaves distinctly flexuose, spirally twisted subulae standing apart at stem apex. Vegetative leaves more or less gradually narrowed into subula, in some leaves sheathing base more distinctly contracted, (2.3–) 2.9–3.1 (–3.6) mm long, subula making up more than 2/3 of leaf length in some leaves, mostly about 2/3; cells of sheathing leaf base very variable in size and form, in upper part mostly 12 µm long, some longer, in middle part (12.5–) 20 (–37.5) µm long, in lower part towards costa 18–35 µm, on average 29 µm long, rather broad (about 12 µm) and eporose to very slightly porose, but in some leaves reaching 50 µm length and more distinctly porose, cells in sheathing part form more or less straight rows, very few cells with curved walls; marginal border not well-developed, not more than one cell row broad, not grading into adjacent lamina, consisting of some thin-walled, more or less hyaline cells; auricles present in some leaves.

According to these features these plants are referred to *D. flexicaule* s. str., but they approach *D. crispatisimum* in 3 characters, notably: leaf shape, subula length, and structure of basal cells.

Judging from single stems of other bryophyte species included in these gatherings (*Ctenidium molluscum* in the tuft of *D. crispatisimum* only; *Scapania callicola* in all tufts of *D. flexicaule* s. str. only), *D. crispatisimum* and *D. flexicaule* probably did not form a mixed stand at the Koloska rocks, because in that case they would be likely to have some bryophyte companion in common. This is of interest,

since evidence on the taxonomic distinctness of Frisvoll's taxa is largely based on the observation of mixed stands (FRISVOLL (1985), see Discussion).

BP 95236 represents another collection from the same site: Dr. A. Boros: Plantae Hungariae exsiccatae. *Ditrichum flexicaule* (Schleich.) Hampe. Comit. Zala (nunc Veszprém). In rupestribus dolomit. sept.-or. "Koloska-sziklák" prope Balatonarács. 20.V.1963, Alt. ca. 250 m. s. m.

It also consists of *D. flexicaule* approaching *D. crispatisimum* in some character states: dry leaves are rather straight, leaf length is up to 4.5 mm, subula length is more than 2/3 of leaf length, and in some leaves basal juxtacostal cells are slightly elongate and slightly porose. Apart from the absence of flagellae and orientation of dry leaves, these plants agree in the other relevant features with those of *D. flexicaule* from the afore-mentioned gatherings from Koloska rocks. Moss companions include *Encalypta streptocarpa*, *Trichostomum brachydontium* and *Campylium calcareum*.

BOROS (1968) mentions the locality Koloska rocks and gives a list of the more interesting bryophytes growing at this dolomitic rock: *Cololejeunea calcaria*, *Scapania calcicola*, *Fissidens dubius* (= *cristatus*), *Trichostomum brachydontium*, *Neckera crispa*, *N. complanata*, *Eurhynchium striatulum* (= *Isothecium files-cens*), *Pseudoleskeella* (= *Leskea*) *catenulata*, *Campylium* (= *Chrysohypnum*) *chrysophyllum*, *Homomallium* (= *Hypnum*) *incurvatum*.

During a recent excursion to Koloska rocks (with B. Papp, in February 2001), all the species mentioned by BOROS (1968) were found, and in addition the following species of liverworts and mosses: *Lejeunea cavifolia*, *Metzgeria furcata*, *Plagiochila porelloides*, *Porella platyphylla*, *Radula complanata*, *Reboulia hemisphaerica*, *Amblystegium serpens*, *Brachythecium salebrosum*, *B. velutinum*, *Bryoerythrophyllum recurvirostrum*, *Bryum capillare*, *Ctenidium molluscum*, *Dicranum scoparium*, *Ditrichum flexicaule* s. str., *Encalypta streptocarpa*, *E. vulgaris*, *Eurhynchium hians*, *Grimmia pulvinata*, *Gymnostomum calcareum*, *Homalia bes-seri*, *Homalotheicum sericeum*, *Hylocomium splendens*, *Hypnum cupressiforme*, *Isothecium alopecuroides*, *Myurella julacea*, *Plagiomnium rostratum*, *P. undulatum*, *Pseudoleskeella nervosa*, *Rhytidiadelphus triquetrus*, *Schistidium crassipilum* H. H. Blom, *Tortella tortuosa*, *Tortula ruralis*, *T. subulata*. Most of these species are frequent in suitable habitats in Hungary, but *Gymnostomum calcareum* and *Myurella julacea* are remarkable and probably would have been mentioned by Boros had he detected them. Although the populations of *D. flexicaule* present in Koloska rocks were carefully examined, no trace of *D. crispatisimum* could actually be found. This species must therefore be considered to be extinct in Hungary.

Plants intermediate between *Ditrichum crispatisimum* and *D. flexicaule*

A few more specimens of *D. flexicaule* were found to display similarities with *D. crispatisimum* in some respects. Apart from the plants from Koloska rocks dealt with above, such transitional plants had been collected in three different localities.

BP 94811. – Dr. A. Boros: Plantae Hungariae exsiccatae. *Ditrichum flexicaule* (Schleich.) Hampe c. set. Comit. Pest. In dolomiticis “Fekete hegyek” prope Budakeszi, versus Telki, 23.VII.1946, Alt. ca. 400 m. s. m.

This specimen contains 3 large tufts of *D. flexicaule* with setae that have lost their capsules. It is referred to this species because of the presence of flagellae, orientation of dry leaves, leaf shape and length, structure of cells in basal sheathing part of leaf and the shape of the innermost perichaetial leaves – characters in typical states of *D. flexicaule*. Features approaching *D. crispatisimum* include length of plants (up to 5 cm), length of subula, and structure of cells towards costa at leaf base (some leaves with porose, elongate cells).

BP 94839. – Dr. A. Boros: Plantae Hungariae exsiccatae. *Ditrichum flexicaule* (Schleich.) Hampe c. sporog. Comit. Borsod. In rupibus calcar. sept. silvat. montis “Nagy István erőse” prope Nagyvisnyő. 29.IX.1950, Alt. ca. 7–800 m. s. m.

This specimen contains altogether 4 moss tufts, but of different appearance: there are two green-yellowish tufts of 4–5 cm long plants without sporophytes, with more or less crisped leaves, labelled (a) for the purpose of reference by the author; and two yellowish slightly shorter tufts with sporophytes and more or less straight leaves, labelled (b). Further distinguishing features include:

(a) leaf length 1.8–2.5 mm, subula less than  $\frac{2}{3}$  of leaf length, juxtacostal basal cells rather short, eporose to slightly porose in most leaves, auricles present.

(b) leaf length 2.2–3.3 mm, subula in some leaves longer than  $\frac{2}{3}$  of leaf length, juxtacostal basal cells elongate, more or less porose in most leaves, auricles not seen, but flagellae present.

(a) is typical *D. flexicaule*. The plants of (b), although approaching *D. crispatisimum* in some character states, viz. subula length and structure of juxtacostal basal cells, can be named *D. flexicaule* because of the presence of flagellae and, especially, the shape of perichaetial leaves.

Since (a) is a pure stand of *Ditrichum*, whereas (b) includes various moss and hepatic companions (e.g. *Ctenidium molluscum*, *Encalypta* sp., cf. *Lophozia* sp.), the different tufts probably did not form part of a mixed stand.

A duplicate (BP 58744) contains two large tufts, 5–6 cm high, similar to (a). Two additional collections had been made at the same locality: BP 21308. – 28.VIII.1951, L. Vajda – 2 tufts of huge plants of *D. flexicaule*, ca 6–7 cm long; BP

94840. – 9.VIII.1953; Á. Boros – *D. flexicaule* with sporophytes, but otherwise unlike (b).

BP 94836. – Dr. A. Boros: Plantae Hungariae exsiccatae. *Ditrichum flexicaule* (Schleich.) Hampe. Comit. Heves. In rupibus andesit. silvat. sept. montis Saskő prope Parád 27.IV.1952. Alt. ca. 8–890 m. s. m. (Duplicates: BP 94837, leg. Á. Boros; BP 94838, leg. Á. Boros; BP 22860, leg. L. Vajda; BP 58739, leg. T. Pócs et I. Gelencsér). This represents a very interesting form of *D. flexicaule* with plants up to 8 cm long., leaves to 4.6 mm long, but otherwise with typical character states of *D. flexicaule*. Originally, Boros and colleagues took it as a variety of *Dicranodontium denudatum*, but H. Persson, to whom the specimen was sent, wrote the following note: “The moss you sent to me is no *Dicranodontium* but a very curious form of *Ditrichum flexicaule*, very unlike what we are used to see. It is somewhat resembling but not identic with fo. *longifolium* (possibly a species, described from Yukon by Williams as *D. giganteum* and believed by the very clever Finnish bryologist M. M. Tuomikoski to be a species) but a parallel form. These very remarkable extreme *flexicaule*-formae have often troubled the bryologists.” (Herman Persson, in litt. 12.VI.1953).

### *Ditrichum flexicaule* in Hungary

The localities of *D. flexicaule* according to the revised specimens are shown in Figure 2. (A list of the specimens can be obtained from the author upon request.)

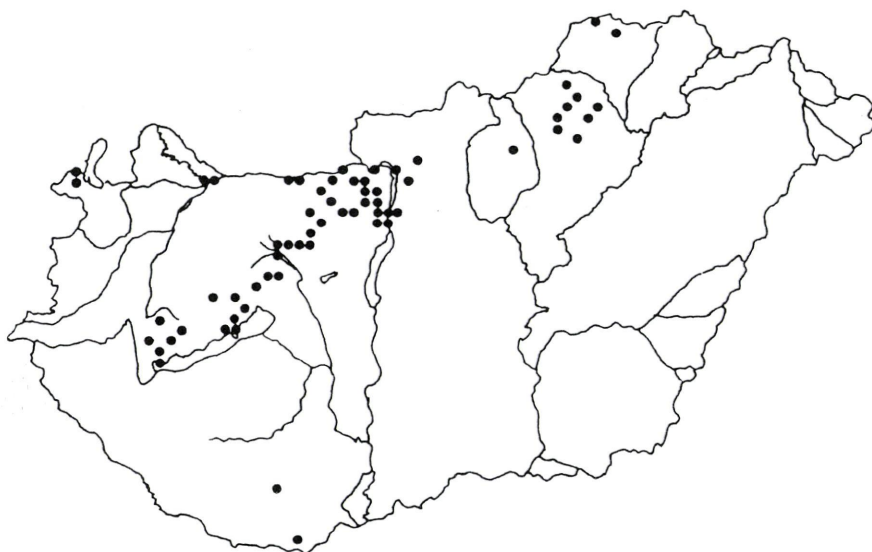
It can be seen that *D. flexicaule* occurs predominantly in the calcareous hills in the northern (Aggteleki-karszt Mts, Cserehát Mts, Bükk Mts, Cserhát Mts, Gödöllő hills), central (Mt Naszály, Pilis Mts, Buda Mts, Gerecse Mts, Vértes Mts), and western (Bakony Mts, Balaton upland, Keszthely Mts) parts of the country, with more isolated records in the northwest near Sopron and in the south (Mecsek Mts, Villány Mts). In mountains of volcanic origin, *D. flexicaule* is rare (Mátra Mts: Sas-kő, Börzsöny Mts: Ördög-hegy/Nagymaros). Even more exceptional are records from sandy hills in lowland areas of the Danube valley: near Győr and Budapest (Káposztásmegyer).

The distribution is in agreement with the data in BOROS (1968), ORBÁN and VAJDA (1983) and ORBÁN (1974), except that there appears to be no specimen from the Zemplén Mts in BP.

Sporophytes of *D. flexicaule* are very rare in Hungary (BOROS 1968). They are obviously overrepresented in collected specimens, because specimens from 19 localities had sporophytes (or at least setae) (Table 2).

**Table 2.** Specimens of *Ditrichum flexicaule* with sporophytes.

| Region         | Locality                               | Year of collection     |
|----------------|----------------------------------------|------------------------|
| Bükk Mts       | Örvény-kő / Mályinka                   | 1951                   |
|                | Nagy István erőse / Nagyvisnyó         | 1950, 1953             |
|                | Uppony                                 | 1934                   |
| Pilis Mts      | Csúcs-hegy / Csobánka                  | 1947                   |
| Naszály Mts    | Vác                                    | 1926                   |
| Buda Mts       | Kis-Szénás / Pilisszentiván            | 1917, 1927, 1946, 1948 |
|                | Alsó-Zsíros-hegy / Pilisszentiván      | 1946                   |
|                | Felső-Zsíros-hegy / Pilisszentiván     | 1946                   |
|                | Fekete-hegyek / Telki                  | 1946                   |
|                | Ló-hegy / Budaörs                      | 1945                   |
| Vértes Mts     | Meszes-völgy / Csákberény              | 1934                   |
|                | Csatorna-völgy / Csákberény            | 1935                   |
|                | Macskagödör (Fáni-völgy) / Vérteskozma | 1932                   |
|                | Gánt                                   | 1936                   |
| Balaton upland | Felsőörs                               | 1957                   |
| Bakony Mts     | Baglyos-kő / Inota                     | 1932                   |

**Fig. 2.** Records of *Ditrichum flexicaule* in Hungary, according to herbarium specimens revised by the author.

## DISCUSSION

In this paper, FRISVOLL's concept (1985) of two species making up the *Ditrichum flexicaule* complex was applied to the specimens collected in Hungary housed in BP. Although the majority of specimens could be named without problems, some were found to be intermediate, in that they approach *D. crispatisimum* in some character states, while in others they exhibit typical features of *D. flexicaule*.

Frisvoll's concept has been applied by other authors to different regions of Europe. While CASAS *et al.* (1990) succeeded in sorting out Spanish specimens into Frisvoll's taxa, other authors admit difficulty (SMITH 1993) or report similar results with respect to seemingly intermediate forms (NOVOTNÝ 1997).

Smith disagrees with Frisvoll on the usefulness of some characters, and in respect to one very important feature – flexuosity of leaves – he even contradicts Frisvoll's result. Since this point, which is also related to the meaning of the specific epithet "*crispatisimum*", is considered very essential, it will be discussed here at some length.

According to FRISVOLL (1985), the leaves of the type of *D. crispatisimum* "are rather strongly crisped (...), probably because it grew in a sheltered place...". But this is not typical of the taxon as conceived by Frisvoll! In general, its leaves are "usually slightly or *not flexuose* (except in some sheltered habitats), ..., often falcate", whereas the leaves of *D. flexicaule* s. str. are "*usually flexuose*, rarely falcate" (Table 2 in FRISVOLL 1985; emphasis added by P. E.). This is in agreement with earlier comments, e.g. in NYHOLM (1954) on *D. flexicaule* var. *sterilis* De Not. (a synonym of *D. crispatisimum*: "leaves almost straight, ... when dry, leaves are not crisped"), and *D. flexicaule* ("leaves ... crisped when dry"), as well as in TUOMIKOSKI *et al.* (1973), stating that leaves in *D. giganteum* Williams (another synonym of *D. crispatisimum*) "are not characteristically bent to somewhat crisped when dry", and in *D. flexicaule* are "somewhat crisped when dry". It is also in agreement with the observations of the author on British, Irish and French specimens including *D. crispatisimum*.

SMITH (1993), on the other hand, states that dry leaves in *D. crispatisimum* are "*usually flexuose*" (p. 45), and a second time "*often flexuose*, sometimes secund" (p. 51), whereas in *D. flexicaule* they are "*rarely flexuose* or secund". He does not seem to have noticed the discrepancy between his and Frisvoll's statements, since he does not comment on this matter. Although the other character states listed by SMITH (1993) are in agreement with FRISVOLL (1985), leaf crispness is a very characteristic feature differentiating *D. flexicaule* and *D. crispatisimum* macroscopically, and since SMITH (1993) also states that "95% of speci-

mens of *D. flexicaule* s. l. could be allocated to one or other of the species with the naked eye or a  $\times 10$  lens", the question arises, whether Smith's results are in fact reliable.

It seems possible that other discrepancies between Smith's and Frisvoll's accounts originate in this misconception. Misidentification of specimens of two closely related taxa could indeed result in what appears to blur boundaries that are in fact more clear-cut, as has happened, e.g. with *Hedwigia stellata* and *H. ciliata*: FRAHM (1995) stated the existence of intermediates between these taxa. His conclusions were, however, based on several misidentified specimens (ERZBERGER 1996a, b).

Smith's comments on the 16 differences listed by Frisvoll, saying that "some are somewhat intangible or ambiguous". Among the characters Smith could not confirm is the structure of cells near the costa at the leaf base. This character, on the other hand, is considered by Frisvoll so important that he includes it in the abstract of his paper as the first of three features differentiating *D. flexicaule* and *D. crispatisimum*, and he comments on it (Table 2 in FRISVOLL 1985): "When naming plants in *D. flexicaule* s. l. more importance should be put on the structure of cells than on cell measurements". This clearly is in contrast with Smith who states that in critical cases naming is possibly only "with difficulty on the basis of summation of characters". The possibility cannot be ruled out that a repeated revision of the material seen by Smith could lead to a different opinion on this and other character states of Frisvoll's taxa in the British Isles. At present, Smith's report cannot be taken as evidence for geographical variation of *D. crispatisimum* in this important feature.

Another point of disagreement between Smith and Frisvoll concerns the relation of length of dorsal cells on the costa and in the adjacent lamina. Smith states that the claimed difference (costa cells longer than lamina cells in *D. flexicaule* and shorter in *D. crispatisimum*) is variable and only sometimes applies in *D. crispatisimum*. Frisvoll himself concedes that in *D. crispatisimum* from northern areas costa cells are "sometimes more elongate". It is interesting to compare his illustrations of this feature (Figs 1, 15 in FRISVOLL 1985) with those (Figs 1F, 2F) of CASAS *et al.* (1990): the difference appears far more pronounced in the Spanish material.

In the Hungarian specimen of *D. crispatisimum*, this character varies among individual leaves of a single plant.

NOVOTNÝ (1997) reports results of a morphometrical analysis of *D. flexicaule* s. l. evaluated by multivariate methods. From his principal component analysis the discriminating power of the characters used by him can be evaluated. How-

ever, a number of shortcomings in the definitions of his characters make it difficult, or even impossible, to apply these results in further studies.

To illustrate this, the characters examined by Novotný will be discussed in detail:

1. "hyacel" = "absolute number of hyaline cells at the edge of leaf base"

According to FRISVOLL (1985), *D. crispatisimum* has (1)2–4 rows of narrow, elongate and frequently pseudohyaline cells in the marginal border of the sheathing leaf base, whereas *D. flexicaule* has (0)1–2 such rows; the border is usually distinctly marked towards the inner lamina cells in *D. flexicaule*, but less marked in *D. crispatisimum*. It is therefore hard to conceive how "hyacel" can be estimated with any accuracy in *D. crispatisimum*. One could speculate that "hyacel" might refer to the number of hyaline cell rows.

2. "curvat" = "curvature of cell wall at leaf base near costa"

Novotný here seems to merge two different features into one. (i) Cells in the middle of the sheathing leaf base differ in shape between the taxa: they are isodiametric or shortly rectangular with straight to slightly curved walls in *D. flexicaule*, and usually elongate with curved walls in *D. crispatisimum*. (ii) Cells at the base along the costa are elongate, eporose or sometimes indistinctly porose in *D. flexicaule*, and longer and porose in *D. crispatisimum*. From the categories ("straight, intermediate, curved") used to scale "curvat" it seems that Novotný is referring to the first feature (i), unless he means porosity of cell walls, which results in cell walls being "curved" in some sense as well.

3. "leafle" = "absolute length of leaf in mm"

4. "awlness" = "awlness [?] of leaf"

To judge from the categories ("not awl-shaped, intermediate, awl-shaped") used to scale "awlness" Novotný seems to be referring to leaf shape, with leaf base rather suddenly narrowed into a comparatively short subula in *D. flexicaule*, and lamina more gradually tapering towards a comparatively long subula in *D. crispatisimum*.

5. "shorte" = "length ratio of cells on costa/cells on leaf edge in its awl-shaped part"

The "awl-shaped part" obviously refers to the sheathing part of the lamina. Novotný does not state more precisely at which part of the leaf length of costa cells is studied. His illustrations – rather schematic representations of this feature – do not elucidate this point either.

6. "tootne" = "denticulation of leaf tip"

7. "tippbre" = "absolute breadth of tip at a distance of 35 µm"

This is an interesting character not mentioned by Frisvoll, related to usually longer and narrower subulae in *D. crispatisimum*.

Of the seven characters used by Novotný four are more or less evident (nrs 3, 5, 6 and 7), three are rather obscure (nrs 1, 2 and 4), but the meaning of one can be guessed (nr 4). In spite of these obvious shortcomings, the application of multivariate methods leads to some interesting results.

According to Novotný's principle component analysis leaf length (3) and shape (4) discriminate strongest between *D. crispatisimum* and *D. flexicaule*. Of slightly less importance seem characters related to the hyaline border (1), to cell structure in the sheathing leaf base (2) and to the relation of costa to lamina cells (5). Characters related to subula apex appear to be least significant in separating taxa: only a fraction of the *D. crispatisimum* specimens show the typical denticulation, and only part of the *D. flexicaule* specimens have a broader subula apex.

Perhaps the most interesting result of Novotný's work is his claim of intermediates. Due to the fact, however, that it is not clear in which way he applied some crucial differentiating characters like porosity of basal juxtacostal cells, it remains open to question whether his so-called "transitive forms" could not in fact be referred to one of Frisvoll's taxa by the consequent application of all features stressed by Frisvoll as important. As an explanation for the existence of intermediates Novotný suggests that *D. crispatisimum* is a relatively young taxon which is separated from *D. flexicaule* by a barrier of different intensity in different parts of its range, without giving further evidence for this.

According to the revision of the Hungarian material presented here, the situation may be similar to the findings of NOVOTNÝ (1997) for the Czech and Slovak Republics: some specimens could be named only with difficulty, due to the fact that they showed a combination of features of both species, or the character states were intermediate or variable.

Perhaps the revision of *D. flexicaule* s. l. from a wider geographical range could elucidate some of these still controversial questions.

Outside of Europe, *D. flexicaule* s. l. occurs in the High Arctic, Subarctic America, North America, Guatemala and Colombia, western South America, Madeira, N Africa, Middle, northern and eastern Asia, Himalayas, Malesia, New Zealand and New Guinea (PORLEY 1992, SEPPELT 1982, BARTRAM 1949, ALLEN *et al.* 1994). MATSUI and IWATSUKI (1990) report *D. crispatisimum* from Japan and Taiwan.

In central America, according to ALLEN *et al.* (1994), there are three intergrading expressions in the *D. flexicaule* complex, associated with the names of *D. gracile* (Mitt.) O. Kuntze, *D. crispatisimum*, and *D. longicaule* Bartr., and related to taxa occurring outside central America like *D. punctulatum* Mitt. and *D. flexicaule* s. str. These authors consider the possibility that this complex represents

a single, extremely variable and widespread taxon. They list *D. crispatisimum* as a synonym of *D. gracile*, a name antedating *D. crispatisimum* by 5 years, and thus *D. gracile* would appear as the correct name. But since the taxonomic relations are not yet clear, at present the name *D. crispatisimum* is preferred in this paper. A worldwide revision is obviously urgently needed.

CRUM and ANDERSON (1981) claimed that all differences in size, appearance and microscopical detail within the *D. flexicaule* complex could be related to habitat conditions, especially shade and moisture. However, FRISVOLL (1985) observed mixed stands in which the taxa were distinct, as had already TUOMIKOSKI *et al.* (1973). FRISVOLL (1985) also enumerates some "mixed collections". The logic of this approach has been criticized by WYATT *et al.* (1982). These authors in particular reject the extension of the method from mixed stands to mixed gatherings in herbarium specimens.

In the Hungarian material of the *D. flexicaule* complex, two "mixed collections" were found, as described above: the single specimen from Koloska rocks containing *D. crispatisimum* together with *D. flexicaule*, and a specimen from Nagy István erőse, containing two forms of *D. flexicaule* differing in appearance and some microscopical details. In both cases, however, judging from the occurrence of companion species in the colonies, these mixed collections probably did not form part of mixed stands. Therefore, no taxonomic conclusions can be drawn from their observation.

DÜLL and MEINUNGER (1989) recognize two varieties in *D. flexicaule* s. l.: var. *flexicaule* and var. *longifolium* (Zett.) Hag., a synonym of *D. crispatisimum* according to FRISVOLL (1985). The distinction of the taxa in question at the varietal level seems more appropriate if the existence of intermediates can be demonstrated on a larger scale. The existing reports of intermediates in the literature are considered here to be of a preliminary nature, mostly for methodological shortcomings, as discussed above. Whether the Hungarian problematic plants described in this paper are only exceptions, as Frisvoll conceives specimens which are hard to name ("aberrant plants or difficult modifications from unusual habitats"; FRISVOLL 1985), or if they represent intermediates that frequently and as a rule occur together with more typical morphs of *D. crispatisimum* and *D. flexicaule*, remains to be resolved by further studies.

\* \* \*

*Acknowledgements* – I am grateful to the curator of BP, Dr B. Papp, for the loan of specimens and for participating in the search for *D. crispatisimum* at Koloska rocks, to the curator of B for the permission to study some specimens, to C. Casas for examining the Hungarian specimen of *D. crispatisimum*, to Gy. Szél for help with preparing the map and to C. Kraft for linguistic corrections.

## REFERENCES

- ALLEN, B., CRUM, H., PURSELL, R. A., ALLEN, N. S. and REESE, W. D. (1994): *Moss Flora of Central America*. Part 1: Sphagnaceae–Calymperaceae. – Missouri Bot. Garden, St. Louis, 242 pp.
- BARTRAM, E. B. (1949): Mosses of Guatemala. – *Fieldiana Botany* **25**, Chicago Natural History Museum, 442 pp.
- BOROS, Á. (1968): *Bryogeographie und Bryoflora Ungarns*. – Akadémiai Kiadó, Budapest, 466 pp.
- CASAS, C. (1991): New checklist of Spanish mosses. – *Orsis* **6**: 3–26.
- CASAS, C., BRUGUÉS, M. and CROS, R. M. (1990): *Ditrichum flexicaule* (Schwaegr.) Hampe y *D. crispatisimum* (C. Muell.) Par. en la península ibérica e islas baleares. – *Botánica pirenaico-cantábrica*, Jaca y Huesca, pp. 35–41.
- CASAS, C., BRUGUÉS, M., CROS, R. M. and SÉRGIO, C. (1992): *Cartografia de Briòfits Península Ibérica y les Illes Balears, Canàries, Açores i Madeira*. (Bryophyte Cartography Iberian Peninsula, Balearic and Canary Islands, Azores and Madeira.) Fasc. III, No. 110, 111: 55–65.
- 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.
- CRUM, H. A. and ANDERSON, L. E. (1981): *Mosses of Eastern North America 1–2*. – Columbia University Press, New York, 1328 pp.
- DÜLL, R. and MEINUNGER, L. (1989): *Deutschlands Moose*. – IDH-Verlag B. Münstereifel, 368 pp.
- ERZBERGER, P. (1996a): Moose Mecklenburg-Vorpommerns VIII: *Hedwigia stellata* Hedenäs. – *Botanischer Rundbrief für Mecklenburg-Vorpommern* **29**: 147–152.
- ERZBERGER, P. (1996b): Zur Verbreitung von *Hedwigia stellata* in Europa. – *Herzogia* **12**: 221–238.
- FRAHM, J.-P. (1995): *Hedwigia stellata* Hedenäs in Deutschland. – *Bryologische Rundbriefe* **20**: 3.
- FRISVOLL, A. A. (1985): Lectotypifications including nomenclatural and taxonomical notes on *Ditrichum flexicaule* sensu lato. – *Bryologist* **88**(1): 31–40.
- 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.
- LUDWIG, G., DÜLL, R., PHILIPPI, G., AHRENS, M., CASPARI, S., KOPERSKI, M., LÜTT, S., SCHULZ, F. and SCHWAB, G. (1996): Rote Liste der Moose (Anthocerophyta et Bryophyta) Deutschlands. – *Schriftenreihe für Vegetationskunde* **28**: 189–306.
- MATSUI, T. and IWATSUKI, Z. (1990): A taxonomic revision of the family Ditrichaceae (Musci) of Japan, Korea and Taiwan. – *J. Hattori Bot. Lab.* **68**: 317–366.
- NOVOTNÝ, I. (1997): Variability and distribution of *Ditrichum flexicaule* sensu lato in the Czech and Slovak Republics. – *Acta Mus. Moraviae*, Sci. nat. **81**: 157–192.
- NYHOLM, E. (1954): *Illustrated Moss Flora of Fennoscandia* II. Musci. Fasc. 1. – Gleerup, Lund, 87 pp.
- ORBÁN, S. (1974): Moos-arealgeographische Studien aus dem Gebiet der Karpaten und Karpatenbecken. II. – *Studia bot. hung.* **9**: 43–70.
- ORBÁN, S. and VAJDA, L. (1983): *Magyarország mohafldrájának kézikönyve*. – Akadémiai Kiadó, Budapest, 518 pp.
- PORLEY, R. D. (1992): *Ditrichum flexicaule* (Schimp.) Hampe. – In: HILL, M. O., PRESTON, C. D. and SMITH, A. J. E. (1992): *Atlas of the Bryophytes of Britain and Ireland*, Vol. 2 Mosses: p. 91.
- SAUER, M. (2000): *Dicranaceae*. – In: NEBEL, M. and PHILIPPI, G. (eds): *Die Moose Baden-Württembergs* **1**: 129–220.

- SEPPELT, R. D. (1982): A monographic revision of the genus *Ditrichum* (Musci: Ditrichaceae). I. Australian and New Zealand Species. – *J. Hattori Bot. Lab.* **51**: 99–150.
- SÉRGIO, C., CASAS, C., BRUGUÉS, M. and CROS, R. M. (1994): *Lista Vermelha dos Briófitos da Península Ibérica*. (Red List of Bryophytes of the Iberian Peninsula). – Instituto da Conservação da Natureza (ICN), Museu, Laboratório e Jardim Botânico, Universidade de Lisboa (MLJB), Lisboa, 45 pp.
- SMITH, A. J. E. (1993): *Ditrichum flexicaule* and *D. crispatissimum* in Great Britain and Ireland. – *Bull. British Bryol. Soc.* **61**: 45–54.
- TUOMIKOSKI, R., KOPONEN, T. and AHTI, T. (1973): The mosses of the island of Newfoundland. – *Ann. Bot. Fenn.* **10**: 217–264.
- WERNER, J. (1999): Première mise à jour critique de la check-list des bryophytes du Grand-Duché de Luxembourg. – *Lejeunia*, N. S., **161**: 3–25.
- WYATT, R., LANE, D. M. and STONEBURNER, A. (1982): The misuse of mixed collections in bryophyte taxonomy. – *Taxon* **31**: 698–704.

(Received: 25 March, 2001)

