

Identification, distribution and a new nothosubspecies of *Trichophorum cespitosum* (L.) Hartman (Cyperaceae) in the British Isles and N. W. Europe

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ABSTRACT

The common form of *Trichophorum cespitosum* (L.) Hartman (Cyperaceae) in Britain and Ireland, growing in acidic peat, is subsp. *germanicum*, while subsp. *cespitosum* is rare in South Northumberland (v.c. 67) in marginal areas of *Sphagnum* mires, with base-enrichment, although specimens exist from elsewhere in Britain and Ireland. The characteristic *Trichophorum* of raised mires in v.c. 67 is a sterile hybrid between subsp. *cespitosum* and subsp. *germanicum*, corresponding to a plant found by E. Foerster in 1970 in the Harz Mountains and elsewhere in N. W. Germany, and for which the name ***Trichophorum cespitosum* (L.) Hartman nothosubsp. foersteri** G. A. Swan, **nothosubsp. nov.** is now proposed. The identification and distributions of these taxa are discussed. Possibly, in earlier times, subsp. *cespitosum* was the plant of raised mires in Britain, as in Norway today, but was displaced by the hybrid except in base-enriched, marginal areas. In Britain, proliferous forms of the hybrid and subsp. *germanicum* also occur.

KEYWORDS: Deergass, raised mires, Harz Mountains, nothosubsp. *foersteri*, floral proliferation.

INTRODUCTION

NOMENCLATURE

The existence of two forms of *Trichophorum cespitosum* (*Scirpus cespitosus* L.), Deergass (Cyperaceae) in Europe was noticed by Palla (1897), who described these as separate species, *T. austriacum* (= *T. cespitosum*) and *T. germanicum*. These species were separated on the basis of sheath character, stem anatomy and geographical distribution, the former being common in Austria and the latter in Germany. In recent years, only in Hess *et al.* (1967) have they been maintained as separate species. In De Filippis (1980) these are given as *Scirpus cespitosus* L. subsp. *cespitosus* and subsp. *germanicus* (Palla) Broddeson, respectively; and in Clapham *et al.* (1987) as *T. cespitosum* (L.) Hartman subsp. *cespitosum* and subsp. *germanicum* (Palla) Hegi, respectively. The use of the generic name *Trichophorum* rather than *Scirpus* is upheld by Salmenkallio & Kukkonen (1989).

Subsp. *cespitosum* has an arctic-alpine distribution and subsp. *germanicum* a Subatlantic distribution according to Oberdorfer (1969). In Hegi (1966) it is stated that they occur in circumpolar and Atlantic-Subatlantic Europe respectively (for distribution maps see Hultén (1962) and Meusel *et al.* (1965)). In Norway, subsp. *germanicum* has a coastal distribution, rising to 850 m, and avoids areas of long snow-cover, according to Fremstad & Skogen (1978), while subsp. *cespitosum* occurs in the mountains. Some overlap of range occurs there, as also in Britain and Germany.

In the northern part of North America the common (circumpolar) plant, growing in acidic peat, is known as *Scirpus cespitosus* L. var. *callosus* Bigelow, which corresponds to the European *T. cespitosum* subsp. *cespitosum* (Bigelow 1824). *S. cespitosus* L. var. *delicatulus* Fernald grows in calcareous habitats, but as it appears to be unrecorded in Europe, it will not be mentioned again in this paper.

The Atlantic-Subatlantic subsp. *germanicum* is not recorded for North America, but Fernald (1921) knew of its existence in Britain, the lower regions of Sweden, Denmark, France and Germany, and stated that in Europe this plant was known as *Scirpus cespitosus*. Possibly this was not surprising as many botanists in Britain (and probably also in the neighbouring countries of low

TABLE 1. CHARACTERS SEPARATING THE TWO SUBSPECIES AND THE HYBRID (ALL NON-PROLIFEROUS) OF *TRICHOPHORUM CESPITOSUM*

Character	Subsp. <i>germanicum</i>	Hybrid	Subsp. <i>cespitosum</i>
Length of spikelet (mm)	3-6		3-4(-5)
Number of flowers per spikelet	8-20		3-7
Length of sheath-opening (mm)	2-3(-5)	1-1.5(-2)	(<1-1)(-1-2)
Length of blade (mm)	3-6	3-7	4-6
Ratio of length of sheath-opening/ length of blade	>0.4	(0.15-0.2-0.35(-0.4))	<0.25
Margin of upper sheath-opening in herbarium specimens	red-dotted	red-dotted	yellowish or yellowish brown
Aerenchyma in stem	+	-	-
Depth of substomatal cavities (μm)	6-7	8-18	20-26
Stomatal length (μm)	42-51	39-46	36.5-40.5
Perianth bristles	papillose		smooth
Excretory cells in old herbarium specimens	+	+	-
Fruiting	+	-	+

+ : present, - : absent

altitude and latitude) failed to realise that their common plant is not *T. cespitosum* subsp. *cespitosum*, but is subsp. *germanicum*. Clearly, however, Fernald (1921) regarded *Scirpus cespitosus* L. as being identical with Palla's *Trichophorum germanicum*, but considered the latter name unnecessary in view of Roth's *S. cespitosus* β *nemorosus* (Roth 1789). However, I do not think that Roth's description identifies the Atlantic-Subatlantic plant.

The crux of the matter concerns whether *Scirpus cespitosus* L. refers to the circumpolar or the Atlantic-Subatlantic plant. The European nomenclature is based on the former, while Fernald suggested that Linnaeus had intended it to be the Atlantic-Subatlantic plant.

There is a specimen (Sheet 71.8) in LINN, but it is believed that this could not have been in Linnaeus' possession until after 1753 and so cannot be considered as an original element for this name, even though it bears the Linnean annotation "cespitosus" (N. J. Turland, pers. comm., 1994). However, the specimen, Herb. Linn. No. 20 (LAPP), is almost certainly the circumpolar plant and can therefore be designated as the lectotype. This will fix the application of the name *Scirpus cespitosus* L. to the circumpolar taxon, i.e. *T. cespitosum* L. subsp. *cespitosum* as it is currently understood in Britain and the rest of Europe. In the present paper I shall continue to follow tradition by using the epithet *germanicum* for the Atlantic-Subatlantic plant.

Fernald's nomenclature has been followed by authors of North American Floras, e.g. Beetle (1947) and Scoggan (1978), as well as in Japan (Koyama 1958). However, Hultén (1962) and Hegi (1966) have reaffirmed acceptance of the European nomenclature.

DISTRIBUTION

In Clapham *et al* (1952, 1962) subsp. *cespitosum* is stated to be known only from Ingleborough and Ben Lawers, but Clapham *et al.* (1987) say "rare and its distribution is imperfectly known". However, in Clapham *et al.* (1981) subsp. *germanicum* is given, quite erroneously, as "rare" and subsp. *cespitosum* as "common".

In Stace (1991) and Kent (1992) subsp. *cespitosum* is omitted, evidently because no clear evidence of its occurrence in the British Isles could be found. Sell & Murrell (1996) state "All our plants seem to be subsp. *germanicum*, for although there are records of subsp. *cespitosum* they have not been substantiated, but plants intermediate between the subspecies have been recorded in widely scattered localities." Nevertheless, in Stace (1997) subsp. *cespitosum* has been reinstated.

In Northumberland subsp. *germanicum* is the common plant, growing in acidic peat in moorland and it appears to tolerate a variety of habitats of varying degree of wetness. However, as I first recognised in May 1988, there is also another plant in Northumberland, which is characteristic of the Border Mires (raised mires), but which also occurs on other *Sphagnum* mires. The distribution

of this is given in Swan (1993), where it was named *T. cespitosum* subsp. *cespitosum*, although queried as being possibly a hybrid. The sheath character of this plant is closer to that of subsp. *cespitosum* than to subsp. *germanicum*.

This plant from Northumberland, which has never been found to produce mature fruits, is now believed to be a sterile hybrid between subsp. *cespitosum* and subsp. *germanicum*, as demonstrated by morphological and anatomical work described in this paper, and confirmed by work using isozyme electrophoresis carried out by P. M. Hollingsworth (Hollingsworth & Swan 1999). A proliferous form also occurs.

Since 1988 I have extensively investigated *T. cespitosum* in Northumberland, but have found subsp. *cespitosum* at only four sites (all in v.c. 67), all less strongly acidic, or base-rich, or less stagnant than those where subsp. *germanicum* or the hybrid occur.

AIMS OF THE WORK

1. To assess critically the values of the various characters which have been used in attempting to identify the three taxa, and where appropriate relating such characters to geographical range.
2. To establish the plant of the Border Mires as being a hybrid.
3. To determine the distributions and habitats of subsp. *cespitosum* and the hybrid in Britain and Ireland and (so far as possible) elsewhere in N. W. Europe, and in particular to resolve the apparent anomaly that in Norway subsp. *cespitosum* is the usual plant of raised mires, whereas in Britain and Germany it is the hybrid.
4. To investigate the distributions and habitats of the proliferous plants.

IDENTIFICATION

GENERAL

Nomenclature of vascular plants follows Kent (1992).

Subsp. *germanicum* is the common plant, forming large, dense tufts, growing in acidic peat, often with *Calluna vulgaris*, *Erica tetralix*, *Juncus squarrosus* and *Molinia caerulea*. The broad lower glume sometimes overtops the comparatively large spikelet, but these characters are not reliable for identification.

The hybrid is less often so densely cespitose as the above and grows in active *Sphagnum* bogs (blanket, raised or valley mires), often with *Andromeda polifolia*, *Calluna vulgaris*, *Drosera rotundifolia*, *Erica tetralix*, *Eriophorum angustifolium*, *E. vaginatum*, *Narthecium ossifragum*, *Vaccinium oxycoccos* and, occasionally, also *Drosera longifolia* and *Rhynchospora alba*.

Subsp. *cespitosum* has very small spikelets. In Northumberland it has not been seen in large, dense tufts; it sometimes occurs in base-rich habitats and never under such strongly acidic or stagnant conditions as the hybrid.

Characters which have been used to separate the three (non-proliferous) taxa are discussed below (followed by a description of proliferous forms) and are summarised in Table 1. Measurements relate to material from Northumberland.

UPPER SHEATH

In subsp. *germanicum* the uppermost sheath has an oblique opening 2–3(–5) mm long and 1 mm broad, the blade being up to 2 × as long as the opening (see key in Foerster 1963).

In subsp. *cespitosum* the opening of the sheath is suborbicular, c. 1 mm in diameter, with the blade 5–10 × as long as the opening. Note that Fremstad & Skogen (1978) give sheath-opening up to 1.5 mm, which overlaps with measurements on the hybrid.

It should be mentioned that in Hegi (1909) the drawings of the sheaths of the two subspecies (Fig. 186, p. 24) have been reversed, although the descriptions (on p. 25) are correct. Even in the third edition of this excellent work (Hegi (1966), Fig. 24, p. 37) this error still remains, which perhaps shows how neglected is *T. cespitosum* [Cinderella of the Cyperaceae!]. However, this character is correctly depicted in Clapham *et al.* (1987) and in Hess *et al.* (1967). Unfortunately in Stace (1997) the sheath characters of the two subspecies have also been reversed.

In the hybrid, the sheath-opening is 1–1.5(–2) mm long, with the blade 3–7 × as long as the opening.

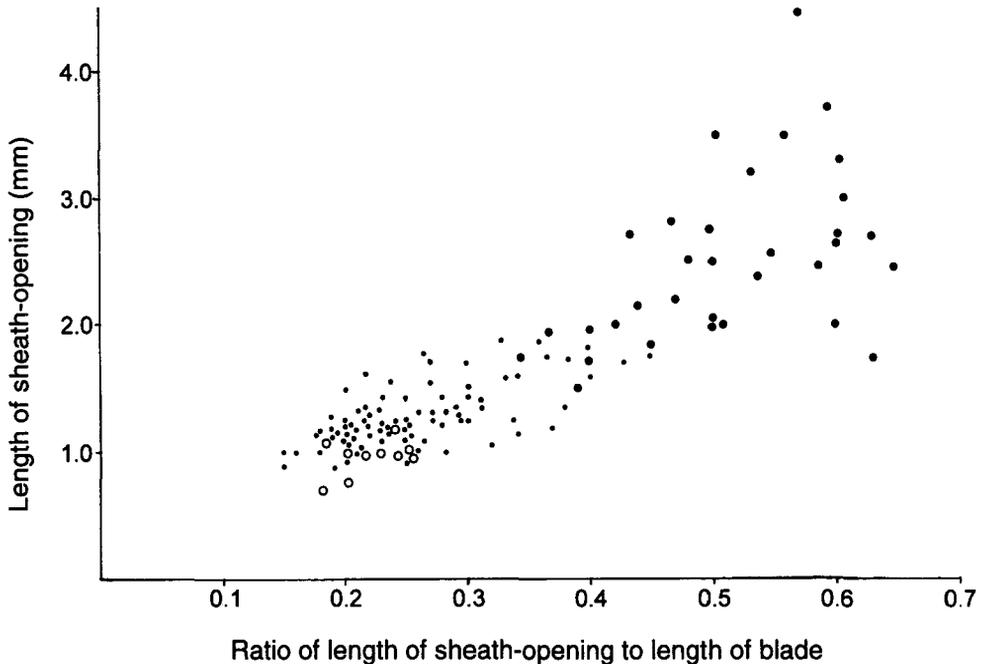


FIGURE 1. Scatter diagram of length of sheath-opening (mm) against ratio of length of sheath-opening to length of blade for *Trichophorum cespitosum* (Northumbrian, non-proliferous, herbarium material). ○ subsp. *cespitosum*, ● subsp. *germanicum*, ■ hybrid.

Fremstad & Skogen (1978) showed diagrammatically the relationship between the length of the sheath-opening and the ratio of sheath-opening to blade length for subsp. *cespitosum* and *germanicum*. Figs 1 & 2 show this relationship in material from Northumberland, including the hybrid, for non-proliferous and proliferous material, respectively. Each point on the diagrams represents the average of three measurements on the same specimen. To see and measure the sheath-opening, it is convenient to first pull out the stem from the sheath.

Palla (1897) and various other authors have contrasted the sheath-opening of subsp. *germanicum* with that of subsp. *cespitosum* as being loose-fitting, with the scarious margin dotted with red or rusty brown, as opposed to close-fitting with the margin yellowish or yellowish brown. However, the first character is relevant only to herbarium material and is likely to be confusing on fresh material (Foerster 1963). Possibly, the presence of aerenchyma in subsp. *germanicum* results in shrinkage of the stem on drying, and hence the appearance of a loose-fitting sheath. The rusty colour is usually very obvious in herbarium specimens of subsp. *germanicum* and often also in those of the hybrid, so its absence can help to confirm subsp. *cespitosum*.

STEM ANATOMY

Cross-sections of fresh stems or dried stem material (the latter soaked in hot water), were cut with a razor blade and examined at $\times 30$. In subsp. *germanicum* aerenchyma is clearly seen (Fig. 3d), whereas in subsp. *cespitosum* it is completely absent (Fig. 3a, 3b). In many specimens of the hybrid, aerenchyma is also absent, although in some there are insular spaces, but not continuous channels (Fig. 3c).

The clearest distinction between the three taxa is seen in the substomatal cavities, best seen at higher magnification ($\times 400$). The stomata run in rows, lengthwise along the stem, and beneath each row of stomata lie the substomatal cavities, which in the case of subsp. *cespitosum* are lined by thick-walled, cutinised cells without chlorophyll. These rows are distributed around the circumference of the stem. In cross-sections of the stem, the substomatal cavities are seen around

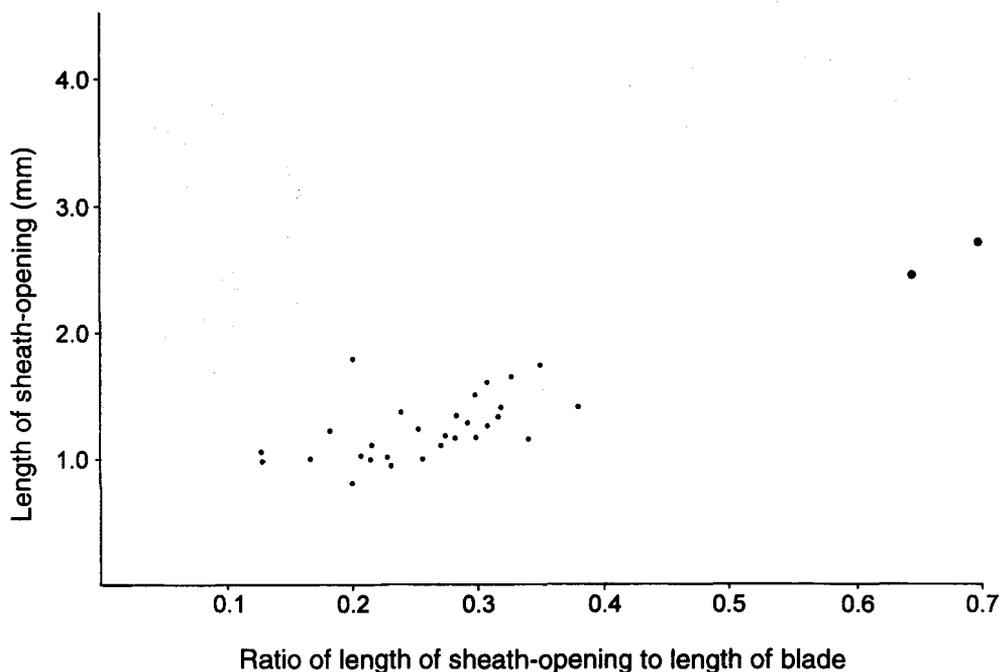


FIGURE 2. Scatter diagram of length of sheath-opening (mm) against ratio of length of sheath-opening to length of blade for *Trichophorum cespitosum* (Northumbrian, proliferous, herbarium material).
 ○ subsp. *cespitosum*, ● subsp. *germanicum*, • hybrid

the periphery, and each with a guard-cell at the outside. The number of cavities through which a particular section cuts varies, but under favourable circumstances it may be up to 12 (some of them double) in subsp. *cespitosum*. The stem cross-sections of the two subspecies are illustrated in Broddeson (1912), and the arrangement of the substomatal cavities in a length of stem as well as the construction of the cavities and guard-cells (in *T. alpinum*) is illustrated in Westermaier (1881). Illustrations of the cavities in subsp. *cespitosum* are given in Montfort (1918) and Metsävainio (1931). There is a good drawing (with scale) of a cross-section showing a substomatal cavity in Firbas (1931), p. 485.

Montfort (1918) showed that, unlike other species of raised mires, *Eriophorum vaginatum* and *T. cespitosum* both have substomatal cavities as described above, the physiological action of which may be to lower rates of transpiration. These cavities increase stomatal resistance and form physiological barriers to transpiration (diffusion pathway lengthened). As a consequence of this structure the plants are anatomically xeromorphic. Both species flower very early, often under semi-frozen conditions, so that the plants may suffer "physiological drought". *Eriophorum latifolium* flowers three to four weeks later than *E. vaginatum*, after the peat has thawed completely and lacks this xeromorphic character. In *T. cespitosum* subsp. *cespitosum* the xeromorphic anatomy is extremely strongly developed, not only in plants from raised mires, but also in other mire systems. The suggestion by Ellenberg (1988) and Lusby & Wright (1996), that the supposed xeromorphic character of bog plants is not true xeromorphism, but is peinomorphism, should perhaps refer only to evergreen ericaceous species. Montfort (1918) suggested that the xeromorphic character of *Eriophorum vaginatum* and *T. cespitosum* subsp. *cespitosum* dates back to the glacial period.

In subsp. *germanicum* (Atlantic-Subatlantic) the substomatal cavities are very small, their radial diameter (6–7 μm) being only half that of the guard-cells, while in subsp. *cespitosum* (circumpolar) they are large, with radial diameter (20–26 μm) up to twice that of the guard-cells. In a good section

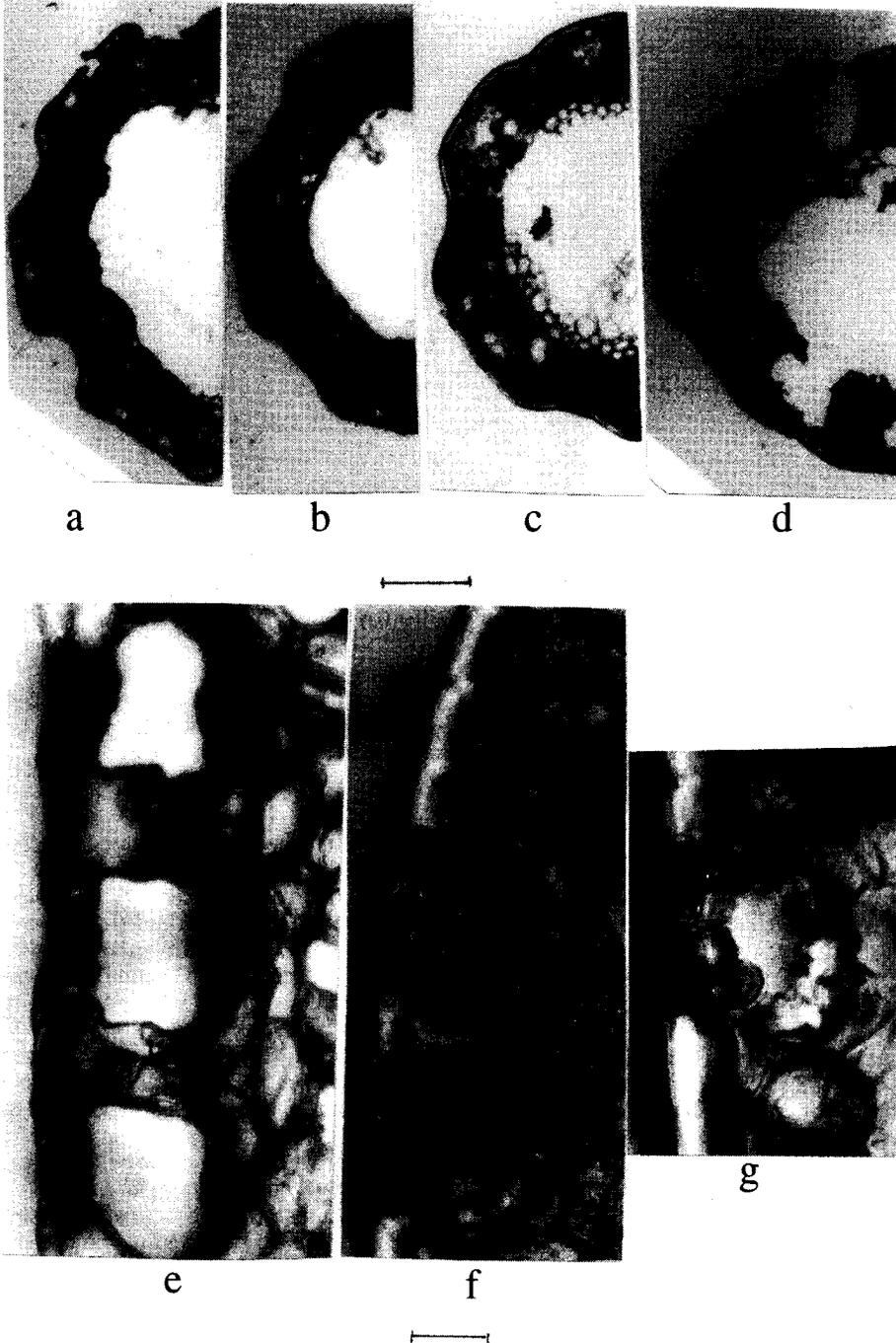


FIGURE 3. Cross-sections of stem of *Trichophorum cespitosum* subsp. *cespitosum* from below Schwarzsee, near Zermatt, Switzerland (a and e), of *T. cespitosum* subsp. *cespitosum* from Blackheugh End, S. Northumberland (v.c. 67) (b and f), of *T. cespitosum* nothosubsp. *foersteri* from Great Wanney Crag Moss, S. Northumberland (v.c. 67) (c and g) and of *T. cespitosum* subsp. *germanicum* from S. Northumberland (v.c. 67) (d). The scale bars represent 0.2 mm (a-d) and 20 μ m (e-g).

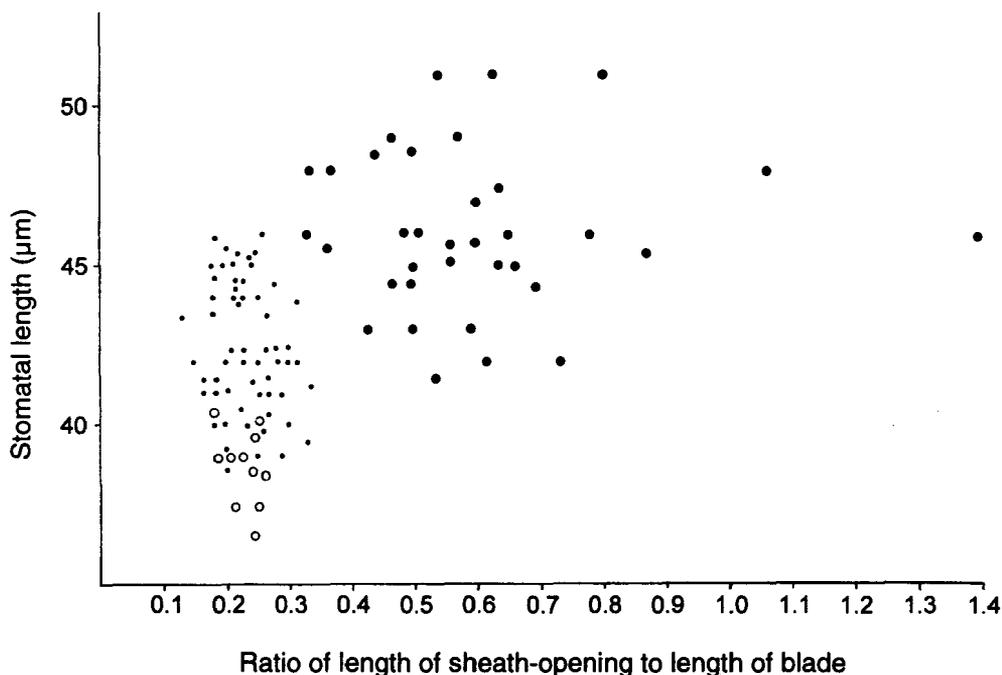


FIGURE 4. Scatter diagram of stomatal length (μm) against ratio of length of sheath-opening to length of blade for *Trichophorum cespitosum* (Northumbrian, non-proliferous, herbarium material) ○ subsp. *cespitosum*, ● subsp. *germanicum*, • hybrid.

of subsp. *cespitosum*, under the microscope these substomatal cavities stand out as a ring of circular (or sometimes slightly squarish) "windows" (some double) around the section. In specimens collected below Schwarzsee, near Zermatt, in Switzerland, at c. 2500 m, the cavities were very large and numerous (Fig. 3a, 3e); in material from Northumberland they were somewhat smaller and less numerous (Fig. 3b, 3f), although the plants were taller than those from the Alps.

In the hybrid the substomatal cavities may be seen as circular (of smaller diameter than in subsp. *cespitosum*) (Fig. 3c, 3g), but more often as oval openings, their depth (towards the centre of the section) (usually 14–17 μm) being less than their width (along the wall of the section) (up to c. 28 μm). The number of cavities seen in a section of the hybrid is usually less than in subsp. *cespitosum*.

The aerenchyma of subsp. *germanicum* is presumably relevant to growth under wet Atlantic-Subatlantic conditions. Examination of a stem-section is an excellent means of separating the three taxa.

STOMATAL LENGTH

Fremstad & Skogen (1978) reported the stomatal lengths as being 48.62 ± 2.39 and 42.29 ± 2.63 μm in subsp. *germanicum* and *cespitosum*, respectively. They showed diagrammatically the relationship between stomatal length and the ratio of the lengths of sheath-opening and blade.

In the present work herbarium specimens of *T. cespitosum* from Northumberland were soaked in hot water before the epidermis was stripped. The lengths of 20 stomata from each specimen (from approximately the middle of a stem) were then measured (at $\times 400$) and the average stomatal length was plotted against the ratio of lengths of sheath-opening to blade, as shown in Figs 4 & 5 for non-proliferous and proliferous material respectively. In agreement with the Norwegian authors, the shortest stomata were found in subsp. *cespitosum* and the longest in subsp. *germanicum*; the hybrid occupied an intermediate position. In a small number of specimens it was found that the average stomatal length varied considerably in different parts of the stem.

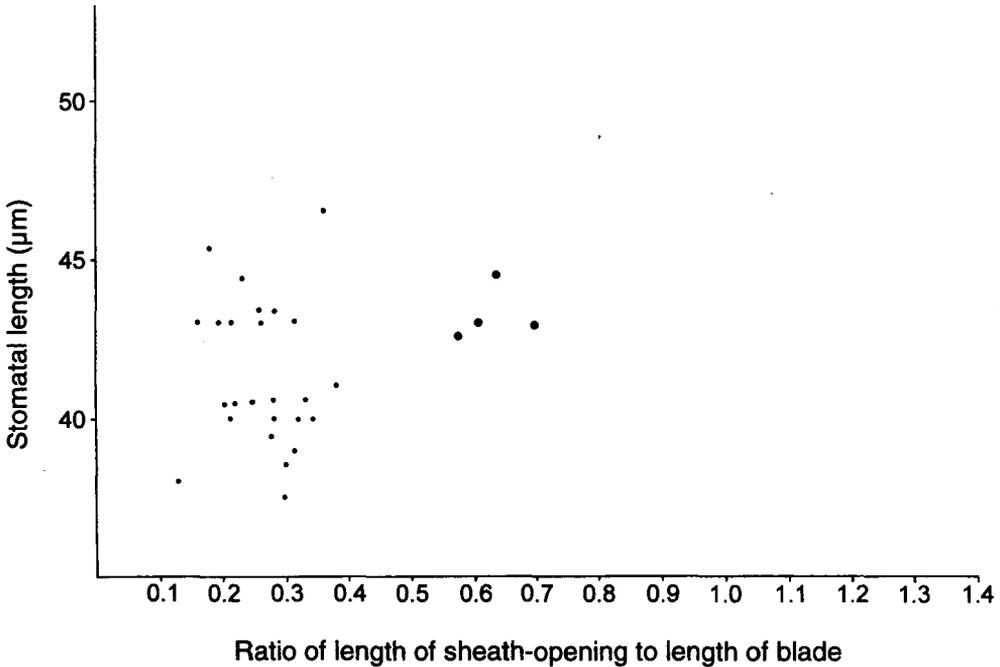


FIGURE 5. Scatter diagram of stomatal length (μm) against ratio of length of sheath-opening to length of blade for *Trichophorum cespitosum* (Northumbrian, proliferous, herbarium material) ● subsp. *germanicum*, • hybrid.

FURROWED STEM

Fremstad & Skogen (1978) stated that whereas the stems of subsp. *germanicum* were furrowed, those of subsp. *cespitosum* were smooth. I noticed that the stems of subsp. *cespitosum* were indeed often only shallowly grooved, while those of the hybrid were usually deeply grooved. However, this character is subject to seasonal variation and is of little value.

PERIANTH BRISTLES

In subsp. *germanicum* the perianth bristles are papillose. In subsp. *cespitosum* they are smooth, except sometimes near the apex.

In agreement with Palla (1897) who recorded this character, I did not find this to be a rigorous means of separation. There are excellent SEM photographs of bristles of the two subspecies in Fremstad & Skogen (1978).

BASAL SHEATHS

Clapham *et al.* (1987) and De Filippis (1980) describe subsp. *germanicum* as having basal sheaths scarcely shining, whilst subsp. *cespitosum* has basal sheaths shining. Sell & Murrell (1996) likewise give "dull" and "shining", respectively.

It is true that when one pulls the plant (e.g. the hybrid) out from a cushion of *Sphagnum*, the basal sheaths are usually shining, but I cannot regard this as a satisfactory character for identification. According to Ostenfeld & Gröntved (1934), the old leaf sheaths in subsp. *germanicum* are "pale-brown, often dark from decaying matter, hardly shining", while in subsp. *cespitosum* they are "bright-brown and shining". This agrees in the main with what is observed in Northumberland, but the difference may merely reflect the different sheath environments (i.e. peat as opposed to living *Sphagnum*) rather than being a character of the subspecies.

EXCRETORY CELLS

Palla (1897) and Fremstad & Skogen (1978) mentioned the presence and absence of excretory cells (red-brown) in the assimilatory tissue of subsp. *germanicum* and *cespitosum*, respectively. In

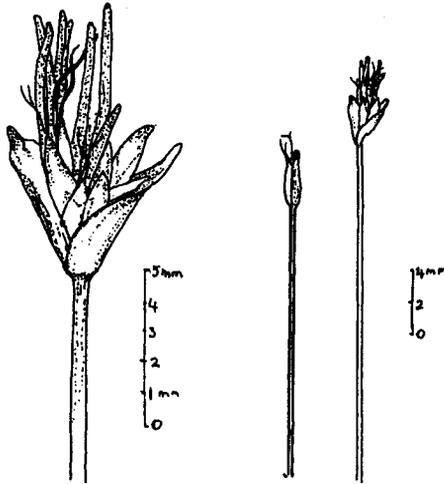


FIGURE 6. Spikelet of proliferous *Trichophorum cespitosum* nothosubsp. *foersteri*.

material from Northumberland these coloured cells were observed only in herbarium specimens which had been kept for at least seven years. Old specimens of either subsp. *germanicum* or the hybrid usually show these red cells, whereas they are absent in subsp. *cespitosum*, so this can be a useful confirmation in the case of herbarium specimens.

FRUITING

Flowering begins in May and, in the case of subsp. *germanicum*, well developed fruits (to c. 2 mm) are formed; spikelets with fruits (containing hard nutlets) and perhaps a few glumes can still be found in August. Subsp. *cespitosum* also produces smaller, short, broad heads of dark fruits. However, in the case of the hybrid, many of the tufts fail to produce fruit at all, and by early July the tops of their stems are more or less bare; in other tufts, development from the flowering to the fruiting stage proceeds and by the beginning of July some small, green, apparently sterile "fruits" (maximum length 1 mm) are present, but soon the glumes are shed. Hard nutlets have never been found.

The flowers of *T. cespitosum* are generally stated to be hermaphrodite, e.g. Clapham *et al.* (1987), Sell & Murrell (1996). However, the last sentence in the account of the species in Hegi (1909) states that some tufts have only protogynous, hermaphrodite flowers, while others have female and male flowers. The occurrence of some tufts with purely male flowers could account for the stems of some Northumberland material becoming bare at the top by early July.

Fruits of subsp. *cespitosum* from the Arctic have been described by Polunin (1959) and in North American plants by Beetle (1947), yet there seems to be a dearth of information on the occurrence or failure of fruiting of subsp. *cespitosum* in Germany and Scandinavia. However, Foerster (1963), on an excursion to the Hohes Venn (near the border between Germany and Belgium) described finding subsp. *cespitosum* on the southern slope of the Pannensterz, where it was growing sparingly among much subsp. *germanicum* and *Molinia caerulea*. He stated that on 27 July 1962 the fruits of the subsp. *cespitosum* there had already fallen and that the subsp. *cespitosum* there was not more delicate than the subsp. *germanicum*, which he suggested might be the result of the stems continuing to lengthen after the ripening of its fruit. In Northumberland the stems of the hybrid continue to lengthen during July and August, even though their tops are bare; and Foerster's observations seem entirely consistent with his plant in the Hohes Venn being the hybrid, rather than subsp. *cespitosum* and having failed to fruit, rather than having dropped its fruits, as stated.

PROLIFEROUS *T. CESPITOSUM*

In raised mires in Northumberland, in addition to the hybrid of *T. cespitosum* subsp. *germanicum* with subsp. *cespitosum*, a proliferous ("viviparous") form of this hybrid also occurs. From the middle of June onwards this can easily be distinguished at sight from the common form, the spikelets being broader and variegated with off-white and green (Fig. 6). This is reminiscent of

TABLE 2. SPECIES GROWING WITH *TRICHOPHORUM CESPITOSUM* SUBSP. *CESPITOSUM* AT BLACKHEUGH END AND GOWANY KNOWE (V.C. 67)

Blackheugh End	Gowany Knowe
<i>Cardamine pratensis</i>	<i>Carex dioica</i>
<i>Carex flacca</i>	<i>Carex hostiana</i>
<i>Carex hostiana</i>	<i>Carex lasiocarpa</i>
<i>Carex panicea</i>	<i>Carex limosa</i>
<i>Carex pulicaris</i>	<i>Carex panicea</i>
<i>Carex rostrata</i>	<i>Carex pulicaris</i>
<i>Carex viridula</i> subsp. <i>brachyrrhyncha</i>	<i>Carex rostrata</i>
<i>Drosera rotundifolia</i>	<i>Carex viridula</i> subsp. <i>brachyrrhyncha</i>
<i>Eleocharis quinqueflora</i>	<i>Dactylorhiza incarnata</i>
<i>Equisetum palustre</i>	<i>Dactylorhiza maculata</i> subsp. <i>ericetorum</i>
<i>Erica tetralix</i>	<i>Drosera rotundifolia</i>
<i>Eriophorum angustifolium</i>	<i>Menyanthes trifoliata</i>
<i>Eriophorum latifolium</i>	<i>Pedicularis palustris</i>
<i>Eriophorum vaginatum</i>	<i>Phragmites australis</i>
<i>Menyanthes trifoliata</i>	<i>Potentilla palustris</i>
<i>Pinguicula vulgaris</i>	<i>Ranunculus flammula</i>
<i>Polygala serpyllifolia</i>	
<i>Potentilla erecta</i>	
<i>Salix repens</i>	
<i>Selaginella selaginoides</i>	
<i>Taraxacum faeroense</i>	
<i>Triglochin palustre</i>	
<i>Vaccinium oxycoccus</i>	
<i>Viola palustris</i>	

Festuca vivipara. The lower flowers in the spikelets develop to form small, sterile "fruits", whereas the upper flowers proliferate to give green plantlets. Also, in all the flowers, the bristles are replaced by a membranous (petaloid) perianth. A particular tuft is either proliferous or non-proliferous, and the proliferous plants usually form smaller tufts than the non-proliferous ones and retain their glumes much longer, so that they can be found up to early September. Even so their "fruits" do not develop much beyond that of the non-proliferous hybrids, and it is unlikely that they ever produce viable seed. Spikelets of the proliferous hybrid, cut off and then planted in peat in late summer, failed to root satisfactorily, but this does not imply that the propagules fail to do so naturally, when they would fall into the *Sphagnum* bog. Although plants of the non-proliferous hybrid grew well in peat in pots, plants of the proliferous hybrid grew less well, rarely producing proliferous spikelets, and sometimes even dying during the winter.

In some mires, only a few tufts of the proliferous form have been found, whereas in others perhaps up to 20% of the tufts are proliferous. The proliferous tufts tend to be clustered together in the same area of the mire.

There is also a proliferous form of subsp. *germanicum*, but this seems to be rare in Northumberland. It was found on 15 August 1995 near Hareshaw Head at NY/856.884, 335 m (v.c. 67), the site probably being a remnant of a raised mire which had been partly drained.

HABITAT OF NON-PROLIFEROUS *T. CESPITOSUM*

The hybrid grows among living *Sphagnum*, while subsp. *germanicum* has less strict habitat requirements and grows in other types of peat bog, some of which were formerly *Sphagnum*-dominated and identical with many surviving *Sphagnum* mires. In Northumberland the hybrid sometimes grows in a rather bare area of bog, accompanied only by *Sphagnum tenellum*. Subsp. *cespitosum* in Northumberland has been found only at the margins of raised or valley mires, where there is some water-movement and base enrichment, never actually within the mire.

LOCALITIES OF SUBSP. *CESPITOSUM* IN NORTHUMBERLAND

Subsp. *cespitosum*, with mature fruits, has been found by G.A.S. at four sites in South Northumberland (v.c. 67). See Table 2.

1. Near Blackheugh End, NY/826.915 (330 m) on 17 July 1995. Here there is a more-or-less flat area of *Sphagnum* mire, with *Drosera rotundifolia*, *Erica tetralix*, *Narthecium ossifragum* and hybrid *T. cespitosum*. Running through this, in an approximately SW/NE direction, is a channel in which grow the species given in Table 2, many of which favour base-rich habitats. It is in this channel that *T. cespitosum* subsp. *cespitosum* grows and where it was first recognised in Northumberland. This site is by the Pennine Way and many walkers pass it, especially during the summer.
2. Gowany Knowe, NY/727.787 (280 m) on 20 July 1996. Gowany Knowe Moss is one of the Border Mires, a raised mire with *Carex magellanica*, *Drosera rotundifolia*, *Narthecium ossifragum*, *Vaccinium oxycoccos* and hybrid *T. cespitosum* (including proliferous material). However, *T. cespitosum* subsp. *cespitosum* does not grow in the raised mire, but by the side of a tiny streamlet at the margin of the mire, only a very short length of which still remains outside the afforested area. This small habitat also has the species listed in Table 2; it is probably rarely visited, although the Moss is a reserve of the Northumberland Wildlife Trust.
3. Head of Bucklake Sike, NY/69.94 (420 m). A specimen was collected by G.A.S. on 28 June 1990 and this appeared to be subsp. *cespitosum*, which was confirmed by the collection of a fruiting specimen on 31 August 1996. Here there is a raised mire containing *Betula nana*, *Calluna vulgaris*, *Carex rostrata*, *Molinia caerulea*, *Polygala serpyllifolia*, *Potentilla erecta*, *Salix repens* and *Vaccinium oxycoccos*. The lower end of this mire is drained by a tiny streamlet containing *Menyanthes trifoliata*, *Carex panicea* and *C. pulicaris* and this is where *T. cespitosum* subsp. *cespitosum* grows. Further downstream *Carex limosa* appears and also *Hammarbya paludosa*, although the latter has not been seen since 1973. Still further downstream is *Potamogeton polygonifolius*. This is a remote site on land owned by the Duke of Northumberland. The proliferous hybrid is also present.
4. Muckle Moss, 4 September 1996. This is a valley mire, which contains the hybrid. Subsp. *cespitosum* was not found in the mire itself, but in the margin ("lagg") at NY/796.670 (230 m), with *Calluna vulgaris* and *Salix repens*. This is a National Nature Reserve and the lagg has been reported to contain *Sphagnum balticum*, *S. majus* and *S. riparium*. Strangely, it is stated in Ratcliffe (1977) that *T. cespitosum* is conspicuously absent in Muckle Moss.

In addition, I investigated many base-rich flushes on peat in Northumberland, each containing several of the species listed in Table 2, but found no *Trichophorum* in any of these.

HABITATS IN SCANDINAVIA

According to Fremstad & Skogen (1978), subsp. *cespitosum* is first and foremost a bog species which occurs throughout Scandinavia (Sjörs 1950). Osvald (1923) has described the occurrence in Sweden of raised mire communities, which appear to be very like those in Northumberland, referred to later in the present paper as *Erica-Sphagnum* mire (National Vegetation Classification M18, Rodwell 1991).

According to Fremstad & Skogen (1978), when subsp. *germanicum* appears in a mire it is usually the result of human influence in the form of peat-digging, burning, grazing or trampling. It also occurs where peat growth has stopped and where it is periodically drier than the normal bog. So, in Scandinavia, subsp. *germanicum* grows commonly with a range of species which are not normally associated with raised mires, such as *Carex binervis*, *Cornus suecica*, *Deschampsia flexuosa*, *Festuca vivipara*, *Luzula multiflora* and *Polygala serpyllifolia* in addition to the normal bog species. Subsp. *germanicum* also occurs on thin peat and at the edge of bogs. The moss cover is poorly developed, the commonest species being *Sphagnum compactum*, *S. molle*, *S. strictum* and *S. tenellum* and other species which thrive where peat growth stagnates. Subsp. *germanicum* also grows on thin peat on paths and trampled places, where peat erosion occurs. According to Fremstad & Skogen (1978), subsp. *germanicum* has never been found in west- or mid-Norway on intact peat bog.

COMPARISON OF HABITATS IN NORTHUMBERLAND AND SCANDINAVIA

From the above, it is seen that subsp. *cespitosum* is the plant which grows in intact peat bogs in Scandinavia, while in Northumberland the hybrid is the characteristic plant in raised mires. There may be two possible explanations for this apparent anomaly.

1. Perhaps subsp. *cespitosum* was once the plant of mires in both Scandinavia and Britain; but with the post-glacial amelioration of the climate, in the British mires it became too warm for subsp. *cespitosum*, so that it could not compete successfully with the hybrid, which gradually replaced it. In Scandinavia, the high altitude and/or latitude of the mires allowed subsp. *cespitosum* to thrive. According to Clapham *et al.* (1987), *T. cespitosum* is absent from base-rich soils in the British Isles, and this does indeed seem to be generally true for subsp. *germanicum*. However, Hegi (1966) and Hess *et al.* (1967) mention calcareous or base-rich habitats for subsp. *cespitosum* in particular. *T. cespitosum* is presumably wind-pollinated and in Northumberland the flowering seasons of the two subspecies probably overlap. Perhaps subsp. *cespitosum* has only escaped extinction through hybridisation by surviving in marginal areas of raised mires, where conditions are sufficiently base-rich to inhibit the growth of subsp. *germanicum*.

2. Possibly the hybrid does in fact occur in at least some mires in Scandinavia, but this has not yet been recognised. In the diagram of sheath-opening against the ratio of sheath-opening to blade length, given (as Fig. 1 on p. 136) in Fremstad & Skogen (1978), the group of records around 1.3/0.3 could represent the hybrid rather than subsp. *cespitosum* (cf. this paper, Fig. 1) and the same could be said of the diagram of stomatal length/ratio of sheath-opening to blade length, given (as Fig. 4 on p. 139), where the group of records around 44/0.2 could represent the hybrid (cf. this paper, Fig. 4). Also in their diagram (Fig. 3 on p. 138), the distribution of stomatal lengths for subsp. *cespitosum* looks as though it might more probably represent a superposition of two taxa (i.e. subsp. *cespitosum* and the hybrid).

Moreover, specimens in **BM** from Norway, Jämtland, marshy ground, 750 m, 2 August 1958, *H. Smith* and in **K**, Norway, Tromsø Island, in a peat bog, July 1921, *V. Summerhayes*, are evidently the hybrid. The northernmost locality yet recorded for subsp. *germanicum* is in Norway, Lofoten (Sortland 1992), somewhat south of Tromsø. There are specimens of what appear to be subsp. *germanicum* from Greenland (**K**); and from Iceland, 17 July 1876, *C. Ostenfeld* (**WU**). Another specimen from Iceland, collected by *N. Polunin* (**BM**) seems to be the hybrid.

In the intact raised mires of the Northumbrian Border Mires, the hybrid is the characteristic and perhaps the only *Trichophorum* present; the community in which it grows is evidently *Erica-Sphagnum* mire [*Erica tetralix-Sphagnum papillosum* raised and blanket mire, *Sphagnum magellanicum-Andromeda polifolia* sub-community (M18)].

According to Fremstad & Skogen (1978), when subsp. *cespitosum* grows in coastal areas of Norway it flowers much earlier than subsp. *germanicum*, thus preventing hybridisation. However in areas of higher altitude and latitude the growing season is short, so that the flowering seasons of the two subspecies overlap, making hybridisation possible. In these areas morphologically intermediate forms have in fact been observed.

Although most of the plants from Northumberland fall fairly clearly into one of the three groups (i.e. subsp. *cespitosum*, subsp. *germanicum* and hybrid) a few have been found with mixed characters. These few have been omitted from Figs 1 & 4; they may correspond to Fremstad & Skogen's (1978) intermediate forms. The hybrid sometimes has good pollen and it is possible that this could cause introgression into subsp. *germanicum*.

DISTRIBUTION

DISTRIBUTION IN NORTHUMBERLAND

In Northumberland subsp. *germanicum* mostly occurs from sea-level to 700 m. The large area of The Cheviot (815 m) above 700 m is virtually free from *Trichophorum*, although on 21 June 1995 I found two small tufts of subsp. *germanicum* on the summit plateau at 800 m. This absence may be a result of the long snow-cover there. In Northumberland the hybrid has been found at altitudes between 215 and 660 m and subsp. *cespitosum* from 230 to 420 m; the upward limits may perhaps

TABLE 3. MIRES IN SOUTH NORTHUMBERLAND (V.C. 67) WITH *TRICHOPHORUM CESPITOSUM* NOTHOSUBSP. *FOERSTERI*

No.	Name of mire	V. c.	Grid reference	Altitude (m)
1	Gowany Knowe Moss	67	NY/730.788	280
2	Felecia Moss	67	NY/721.775	310
3	Harelaw Moss	67	NY/757.771	275
4	Haining Head Moss	67	NY/714.748	260
5	Wedges Rigg Moss	67	NY/712.742	260
6	Hummell Knowe Moss	67	NY/705.714	250
7	Bell Crag Flow	67	NY/763.721	310
8	Coom Rigg Moss	67	NY/689.795	320
9	Muckle Samuel's Crags Moss	67	NY/678.789	300
10	Grain Heads Moss	67	NY/744.735	280
11	Butterburn Flow	70	NY/662.761	280
12	The Flothers	67	NY/699.763	290
13	Limy Sike Moss	67	NY/696.770	280
14	Ottercops Moss	67	NY/948.895	310
15	Drowning Flow	67	NY/760.975	405
16*	Horse Hill Moss	67	NY/765.790	250]
17	Hobb's Flow	67	NY/569.902	380
18	Great Wanney Crag Moss	67	NY/938.834	275
19	Pundershaw Moss	67	NY/775.792	245
20	Sweethope Moss	67	NY/944.817	250
21	Peterstone Flow	67	NY/980.918	320
22	Towey Moss	67	NY/734.555	470
23	Falstone Moss	67	NY/708.860	250
24	Muckle Moss	67	NY/796.670	230
25	The Lakes	67	NY/740.773	285
26	Blackaburn Lough Moss	67	NY/765.795	265
27	Crane Moss	67	NT/911.034	250
28	Beldon Cleugh Moss	67	NY/917.504	365

* Site 16 was searched for *Trichophorum* sp. but none was found.

be due to the absence of *Sphagnum* mires at higher altitude. The hybrid occurs in most intact raised mires in Northumberland, notably the Border Mires (see Lunn & Lunn 1976), but can also be found in other places of higher altitude where *Sphagnum* cover is less continuous, e.g. near the summit of Windy Gyle (NT/855.152) at 600 m, where there is also some *Narthecium ossifragum*, or Scotsman's Knowe (NT/904.191) at 660 m. I also found the hybrid in 1995, just over the border (in Cumberland, v.c. 70) on the N.W. slope of Cold Fell (NY/60.56) at 520 m, growing not in *Sphagnum*, but in *Dicranum scoparium*.

The proliferous form of the hybrid was first noticed on Haining Head Moss (Table 3, Mire 4) on 13 June 1992, although an indeterminate specimen of a proliferous plant, collected on Harbottle Moor (v.c. 67) on 12 August 1934 by G. W. Temperley was later found in HAMU. During the summers of 1993 and 1994 I sought the proliferous hybrid in the 28 mires, thought to be relatively undisturbed, listed in Tables 3 & 4, as well as elsewhere in Northumberland. All these mires were found to contain *Drosera rotundifolia*, *Narthecium ossifragum* and *Vaccinium oxycoccos*. Mires 1–23 are essentially of the blanket or raised mire type, while 24–28 are more of the valley mire type. Mires 1–16 also contain *Andromeda polifolia*, hybrid *Trichophorum* and proliferous hybrid *Trichophorum*, with the exception of Mire 16, which lacks any *Trichophorum* at all and although it was in the same area and was otherwise similar to many others, it had been ploughed up by the Forestry Commission around 1949, but never planted with trees.

Mire 23 is very dry and lacks *Andromeda polifolia* and the proliferous *Trichophorum*.

The proliferous *Trichophorum* hybrid was not found in any of the valley mires, i.e. Mires 24–28, all of which contain the non-proliferous hybrid. Rose (1953) in comparing lowland British valley

TABLE 4. SPECIES ACCOMPANYING *TRICHOPHORUM CESPITOSUM* NOTHOSUBSP. *FOERSTERI* IN THE MIRES IN TABLE 3

Species	Mire no.																												
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	
	blanket or raised mire																							valley mire					
Non-proliferous hybrid <i>Trichophorum</i>	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•	•
Proliferous hybrid <i>Trichophorum</i>	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•											
<i>Drosera rotundifolia</i>	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Narthecium ossifragum</i>	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Vaccinium oxycoccos</i>	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Andromeda polifolia</i>	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•									•				
<i>Drosera longifolia</i>		•		•		•					•																		
<i>Rhynchospora alba</i>				•		•					•																		

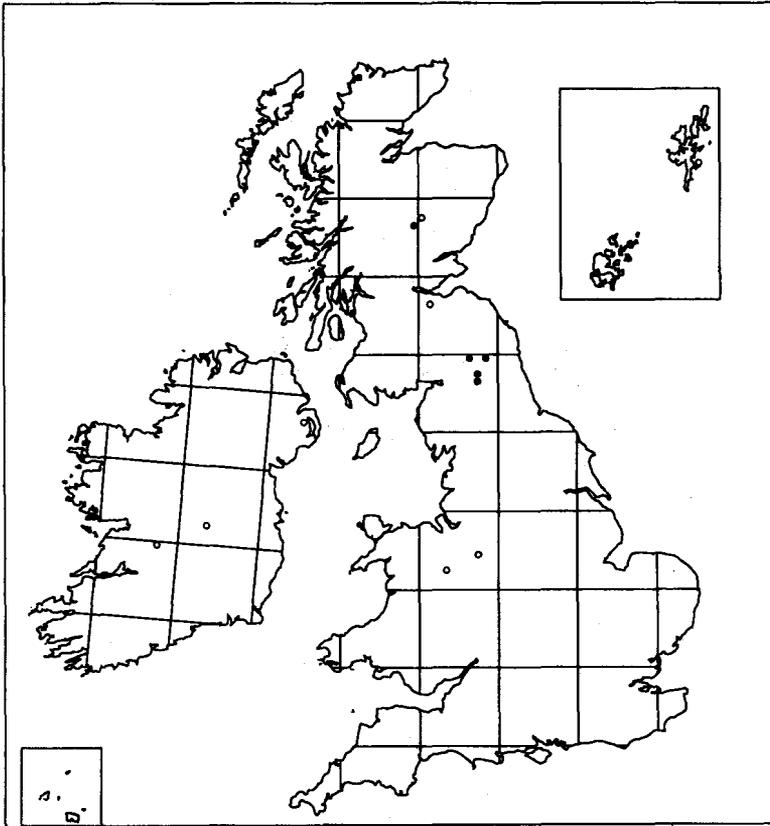


FIGURE 7. The distribution of *T. cespitosum* subsp. *cespitosum* in the British Isles, based on records in 1995–1997 (●) and herbarium records (○).

bogs with raised bogs, stated that the latter are of much greater age than the former; could the proliferous hybrid be a glacial relic? On the other hand, proliferation may be merely environmentally induced. For example, Lawrence (1945) showed that plants of *Deschampsia cespitosa* from Scandinavia, when transplanted to California, became proliferous.

In Coom Rigg Moss (Mire 8), apart from the usual proliferous form with a petaloid perianth, in one area were found many plants of a proliferous form with ordinary bristles.

One tuft of the proliferous plant was found on 16 July 1994 at a site quite different from any of the above. This was on a peaty, grassy slope on Carter Fell (v.c. 67) at an altitude of 550 m, at NT/687.062. This had short stomata like subsp. *cespitosum*, although its substomatal cavities were slightly less deep than those of the latter. This plant requires further investigation as it could be proliferous subsp. *cespitosum*, rather than the proliferous hybrid.

DISTRIBUTION IN THE BRITISH ISLES

Collections of *T. cespitosum* at BEL, BM, DBN, E, HAMU, K, LIV, NMW, PTH and SUN were searched and British specimens which, from visual inspection (without interfering with the specimen) appeared to be either subsp. *cespitosum* (Fig. 7) or the hybrid (Fig. 8) and for which it was possible to give an approximate grid reference, were mapped, along with my records (mainly from Northumberland). Among the herbarium specimens were a few of the proliferous hybrid and proliferous subsp. *germanicum* and these were mapped, along with the corresponding G.A.S. records (Fig. 9). Herbarium specimens of non-proliferous subsp. *germanicum* were also mapped for comparison (Fig. 10). Identifications of the hybrid and subsp. *cespitosum* were checked by cutting stem-sections, when permission to do so was granted.

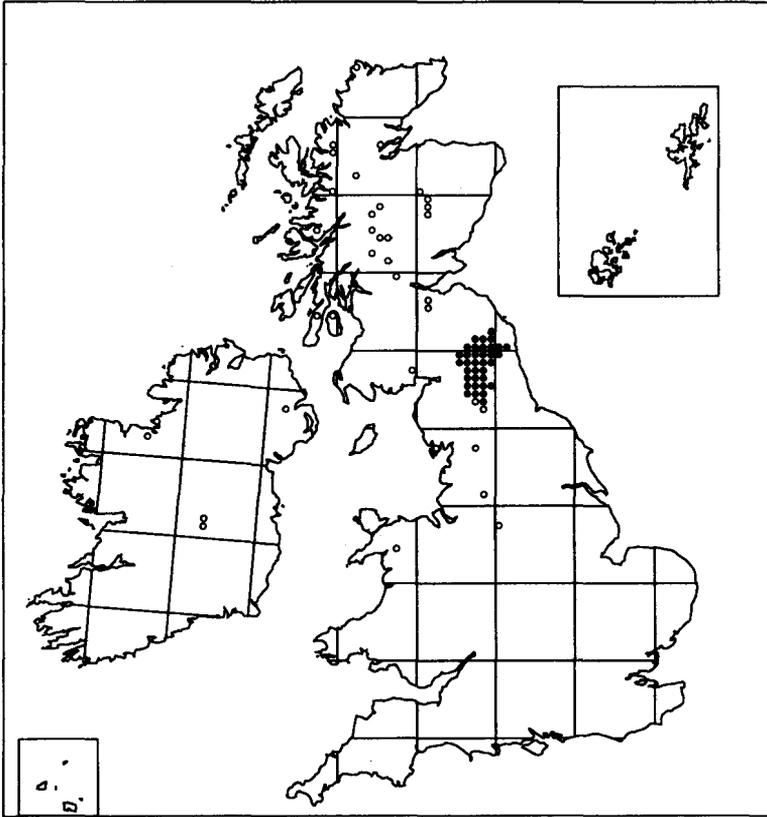


FIGURE 8. The distribution of non-proliferous *Trichophorum cespitosum* nothosubsp. *foersteri* in the British Isles, based on records by G.A.S. in 1988–1996 (●) and herbarium records (○).

HERBARIUM SPECIMENS OF SUBSP. *CESPITOSUM*

Very few specimens which were clearly subsp. *cespitosum* were found, and these are detailed below. Many of them are at low altitude and not in areas of the highest rainfall.

v.c. 40, Salop, Twyford Vownog, near West Felton (SJ/3.2), 26 June 1840, *W. A. Leighton* (BM).

A good, fruiting specimen. Also in E*.

v.c. 58, Cheshire, Wybunbury Moss (SJ/7.4), 27 August 1892, *J. E. Nowers* (SUN).

v.c. 83, Midlothian, Balerno Common (NT/1.6), May 1878, *M. W. Evans* (E)*, also June 1931, *W. R. McNab* (DBN).

v.c. 89, East Perth, Ben Vuroch, (c. NO/0.7), 24 July 1884, *J. Brebner* (PTH).

v.c. 112, Shetland, Bressay (HU/5.4) (NMW), with insular aerenchyma.

v.c. H15, S. E. Galway, bog on shore of Lough Derg, near Woodford (R/74.99), 22 June 1898 (DBN).

v.c. H18, Offaly, bog near Tullamore (N/34.25), 25 May 1895, *R. L. Praeger* (DBN).

v.c. H38, Co. Down, Ballygowan (J/43.64), bogs, June 1903, *C. H. Waddell* (BEL).

*These specimens in E had already been recognised and annotated as subsp. *cespitosum* by Dr H. A. P. Ingram in 1963.

HERBARIUM SPECIMENS OF THE NON-PROLIFEROUS HYBRID

v.c. 48, Merioneth, Llyn Morwynion, Ffestiniog (SH/7.4), 21 May 1938, *N. Woodhead* (NMW).

v.c. 57, Derbys., Goyt's Moss, Buxton (SK/0.7), May 1883, *C. T. Green* (LIV).

v.c. 59, S. Lancs., Ashworth Moor (SD/8.1), July 1853, *Miss Graham* (LIV).

v.c. 64, Mid-W. Yorks., moorland on Ingleborough (SD/7.7), 31 May 1953, *V. Gordon* (LIV).

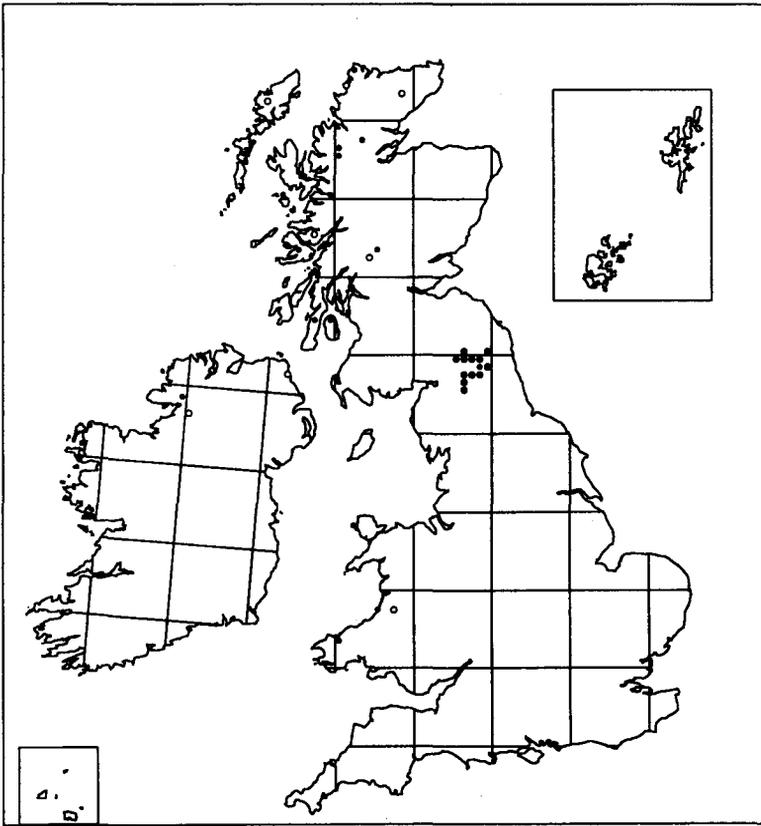


FIGURE 9. The distribution of proliferous *Trichophorum cespitosum* nothosubsp. *foersteri* in the British Isles, based on records by G.A.S. in 1992–1996 (●) and herbarium records (○); and of proliferous subspecies *germanicum* (◐), all herbarium records, except for that at NY/8.8, which is by G.A.S. in 1995.

- v.c. 66, Co. Durham, Widdybank Fell (NY/8.2), 14 July 1905, *T. J. Foggitt* (BM).
v.c. 67, S. Northumb., Fozy Moss (NY/8.7), 17 May 1957, *E. F. Greenwood* (LIV).
v.c. 69, Westmorland, flush in blanket bog, 1 mile [1.6 km] S.W. of Moor House (NY/7.3), 1 September 1956, *F. Rose* (NMW).
v.c. 69b, Furness, Foulshaw Moss (SD/2.7), 10 May 1913, *R. S. Adamson* (BM).
v.c. 70, Cumberland, Butterburn Flow (NY/6.7), June 1964, *F. Rose* (NMW).
v.c. 72, Dumfries, Lochmaben Moss (NY/0.8), *R. Boyle* (LIV).
v.c. 83, Midlothian, Threipmuir (NT/1.6), 31 May 1834; Auchencorth Moss, near Penicuik (NT/19.55), June 1870, *W. Evans* (E).
v.c. 87, W. Perth, Blair Drummond Moss (NS/7.9), 1 July 1882, *F. B. White* (PTH); bog near the col between Am Binnein and Ben More at 1700 feet [520 m] (NN/4.2), 29 July 1914, *E. S. Marshall* (BM, NMW).
v.c. 88, Mid Perth, Stuc a' Chroin, above 2800 feet [850 m] (NN/6.1), 16 July 1885, *F. B. White* (PTH); Breadalbane, July 1885, *W. B. Waterfall* (K); Ben Heasgarnich (NN/4.3), 20 July 1886, *F. B. White* (PTH); Rannoch Moor, near station, 950 feet [290 m] (NN/4.5), 26 June 1936, *J. E. Lousley* (NMW); wet moors near Ben Lawers (NN/6.4), 16 June 1946 (LIV); Ben Lawers (NN/6.4), 24 June 1950, *V. Gordon* (LIV); Ben Lawers, W side of N ridge, 3400 feet [1050 m] (NN/6.4), 14 July 1954, *A. W. Stelfox* (LIV); Craig Laoghain, N of Meall Ghaordie, with *Carex saxatilis*, *C. nigra* and *Eriophorum angustifolium* (NN/515.406), 700 m, 16 July 1981, *A. C. Jermy*, *K. P. Kavanagh* & *A. M. Paul* (BM).
v.c. 89, E. Perth, Gleann Beag, above 1100 feet [335 m] (NO/1.7), 14 July 1885, *A. Sturrock* (PTH).

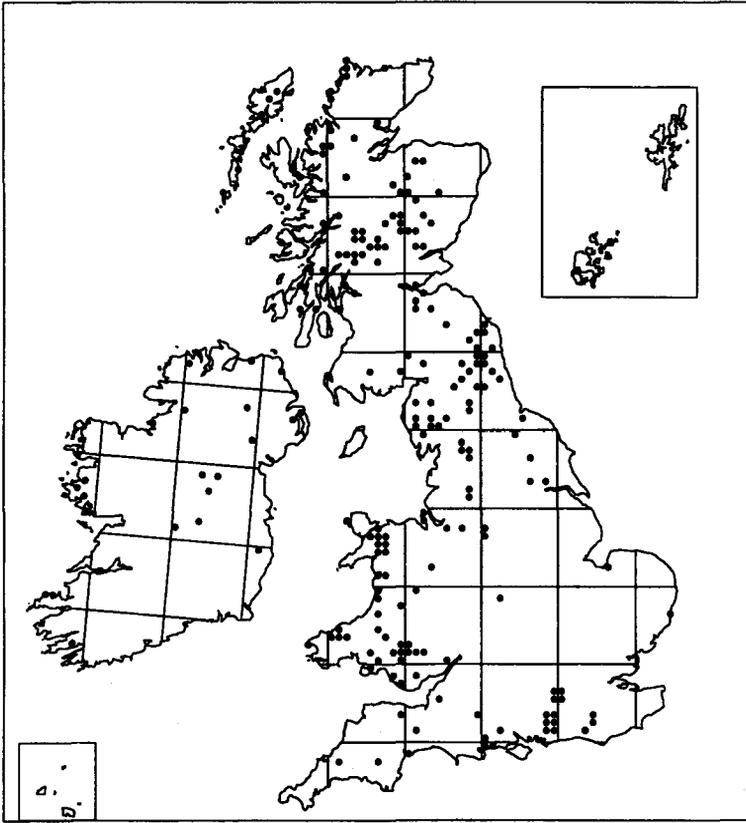


FIGURE 10. The distribution of specimens of *Trichophorum cespitosum* subsp. *germanicum* which were found in the herbaria from which the records in Figs 7, 8 and 9 were derived.

- v.c. 92, S. Aberdeen, end of Loch Callater (NO/1.8), 24 July 1882, *F. J. Hanbury* (BM); Linbrig, near Braemar (NO/1.9), 19 July 1885, *F. J. Hanbury* (BM).
- v.c. 94, Banffs, Cairngorms, Coire Raibiert, 3500 feet [1050 m] (NJ/0.0), 21 July 1966, *E. Rosser* (E).
- v.c. 96, Easternness, Glen Affric, N.E. of Loch Beneveian, among *Sphagnum* in wet slope in birch wood, 740 feet [225 m] (NH/2.2), 13 July 1947, *E. Milne-Redhead* (K); Cairngorm, peat bog, 2300 feet [700 m] (NJ/0.0?), 23 June 1964, *J. K. Smith* (LIV).
- v.c. 97, Westernness, marshes by the wood 3–4 miles [5–7 km] E. of Loch Laggan Hotel (NN/5.8), 15 July 1915, *F. J. Hanbury* (BM); Loch Hourhead (NG/9.0), 7 July 1949, *M. S. Campbell & A. R. Clapham* (BM); Glen Dubh near Alltachonaich, Morven (NM/7.5), 5 July 1973, *S. S. Hooper & C. C. Townsend* (K).
- v.c.100, Clyde Is., Beinn `a Chliabhain, Arran (NR/9.4), June 1890, *A. Somerville* (E).
- v.c. 101, Kintyre, Killean (NR/7.4), 1934, *E. M. Hall* (E).
- v.c. 105, W. Ross, small lochan to S of Loch Maree Hotel (NG/9.6), 21 July 1931, *A. J. Wilmott* (BM); Beinn Eighe Reserve, Allt Coir `a Laoigh, c. 400 feet [120 m], bog by road (NG/977.580), 30 June 1952, *B. W. Ribbons, R. J. Fenn, J. T. Forrest & T. T. Mac Connell* (E).
- v.c. 106, E. Ross, Swordale, moorland, 1100 feet [335 m] (NH/5.6), *A. Meinertzhagen* (BM).
- v.c. 108, W. Sutherland, Loch Aisa to Sandwood Loch (NC/2.6), 14 June 1949, *E. B. & J. F. Basdon* (BM).
- v.c. 110, Outer Hebrides, Lewis, *R. Vowell* (DBN).
- v.c. H18, Offaly, Tullamore (N/34.25), bog, 25 May 1895, *R. L. Praeger* (DBN).

- v.c. H20, Co. Wicklow, Wicklow, *R. Barrington* (DBN).
 v.c. H25, Co. Roscommon, 1848 (DBN).
 v.c. H28, Co. Sligo, Knocknarea (G/50.27), June 1860, *Moore* (DBN); Rock Mountain, wet heath, August 1894, *R. L. Praeger* (DBN).
 v.c. H39, Co Antrim, Black Mountain, Belfast, 10 June 1878, *S. A. Stewart* (BEL). Also in DBN.

HERBARIUM SPECIMENS OF THE PROLIFEROUS HYBRID

- v.c. 46, Cards., on a small flush below the forestry road, 500 m W of Bryn Mawr and 1.5 km S.E. of Hafod, with *Rhynchospora alba*, *Carex dioica*, *Drosera* spp. and *Eriophorum angustifolium*, 1100 feet [335 m] (SN/769.721), 31 August 1963, *A. O. Chater* (NMW).
 v.c. 87, W. Perth, Monachyle Glen, Balquhiddy (NN/4.2), 25 August 1902, *W. E. Evans* (E).
 v.c. 97, Westernness, Glen Dubh, near Alltachonaich, Morven (NM/7.5), 5 July 1973, *S. S. Hooper & C. C. Townsend* (K).
 v.c. 107, E. Sutherland, hill N.E. of Achentoul Lodge, W. of Kinbrace station, in *Erica tetralix*, *Calluna vulgaris*, *Myrica gale* and *Narthecium ossifragum*, 550 feet [170 m] (NC/8.3), 9 July 1963, *V. B. Summerhayes & P. F. Hunt* (K).
 v.c. 108, W. Sutherland, Scourie (NC/1.4), 14 July 1885, *F. J. Hanbury* (BM).
 v.c. 110, Outer Hebrides, Lewis (NB/1.2), two sites, *E. F. Warburg* (BM).
 v.c. H33, Fermanagh, bog at Shea North (H/0.6), c. 1500 feet [460 m], 14 July 1954, *R. D. Meikle* (K).
 v.c. H39, Co. Antrim, Garron Plateau, 14 July 1979, *Dr Ledsham* (BEL).

HERBARIUM SPECIMENS OF PROLIFEROUS SUBSP. GERMANICUM

- v.c. 45, Pembs., bogs on Prescelly Mountains (SN/0.3), 9 September 1932, *C. I. & N. Y. Sandwith* (K).
 v.c. 46, Cards., Rhos Rhudd Bog near Berth Rhys (SN/5.7), July 1958, *G. T. Goodman* (NMW).
 v.c. 88, Mid Perth, Killin (NN/5.3), 14 August 1918 (E).
 v.c. 97, Westernness, Loch Hourhead (NG/9.0), 3 July 1949, *M. S. Campbell* (BM). Specimen unsatisfactory.
 v.c. 100, Clyde Is., Gleann Easan Biorach, Arran (NR/952.475), boggy moorland, 27 August 1951, *R. S. Green* (E).
 v.c. 101, Kintyre, Killean, Kintyre (NR/7.4), 1934, *E. M. Hull* (E).
 v.c. 103, Mid Ebudes, bog between two small lochans, near Benmore Lodge, Salen, Mull (NM/556.372), 15 July 1965, *H. McAllister* (BM).
 v.c. 104, N. Ebudes, W. side of Mullach Mor by Kilmory Glen, Rhum, peat bog on sandstone (NG/3.0), 27 July 1959, *A. C. Jermy* (BM).
 v.c. 105, W. Ross, Kinlochewe (NH/0.6), 18 July 1931, and bog above hotel, 22 July 1931, *A. J. Wilmott* (BM); above Achnashellach, near the Clair Loch (NH/0.5) 4 August 1936, *S. Sanderson* (BM); Allt a` Chiurn, c. 900 feet [275 m], flushed marshy area (NH/003.609), 23 June 1952, *A. L. C. Robertson & D. G. Moulten* (E); An Teallach, c. 1000 feet [305 m], boggy ground (NH/0.8), 1974 (E).
 v.c. 106, E. Ross, flush by road, Glascarnoch reservoir (NH/3.7), 21 July 1971, *U. Duncan* (E).
 v.c. 108, W. Sutherland, S. of Sandwood Loch (NC/2.6), peat bank, 9 July 1948, *P. Marler* (E).
 v.c. H35, W. Donegal, Banagher Hill, N. of Donegal town (G/9.8), rough grazing, upland, 15 July 1970 (DBN).

OTHER HERBARIUM SPECIMENS

The following proliferous specimen has substomatal cavities like the hybrid (14 µm depth), but has a long sheath-opening, with aerenchyma islands and a petaloid perianth:

- v.c. 69, Westmorland, Swindale, S. side of Swindale Foot Craggs (NY/517.138), 360 m, in peat bog with *Eriophorum angustifolium*, *Erica tetralix* and *Sphagnum*, pools with *Utricularia minor*, 3 August 1994, *R. W. M. Corner* (Herb. G.A.S.).

The following non-proliferous specimen has substomatal cavities like subsp. *cespitosum*, but has a long sheath-opening:

- v.c. H18, Offaly, Seagull Bog, a few miles S. of Tullamore (N/3.2), May 1895 (DBN); see Praeger (1894).

Specimens were found of non-proliferous subsp. *germanicum* from v.cc. H8, 18, 20, 25, 28, 29, 30, 33, 39 and 40 without locality. In addition, very many herbarium specimens are not included because the locality could not be deciphered from the label.

LITERATURE RECORDS

Subsp. *cespitosum* has been recorded in the mire at Tregaron (Godwin & Conway 1939), in Meathop Moss (Ostenfeld 1912) and Flanders Moss (Professor A. Skogen, pers. comm., 1992), but in the absence of voucher specimens, it seems more likely that the plant would be the hybrid, as is the case in the Northumberland mires (M18). In other cases, such as the Silver Flow in Galloway (Ratcliffe & Walker 1958), and mires of Stainmore (Pearsall 1941), Cheshire and Shropshire and Flint (Hardy 1939), the subspecies of the *Trichophorum* is not stated. Moore (1968) allotted subsp. *germanicum* to the association in such mires, but this must surely be an error.

RECENT RECORDS FROM SCOTLAND

Wheeler *et al.* (1983) have described how in Perthshire *Schoenus ferrugineus* grows in base-rich flushes in a mosaic of runnels and stony hummocks. On 4 June 1997, Dr R. A. H. Smith kindly collected (at my request) two specimens of *Trichophorum cespitosum* from one such site in Mid Perth (v.c. 88) (B). One stem, collected from an area which was relatively less base-rich, with *Erica tetralix* and *Myrica gale*, was subsp. *germanicum*. The other stem, from a highly calcareous area, with *Carex hostiana*, *C. panicea*, *Eriophorum latifolium* and *Pinguicula vulgaris* appeared to be subsp. *cespitosum*, although final confirmation awaits finding a fruiting specimen.

On 22 September 1997, Dr Smith collected a fruiting specimen from a second such *Schoenus ferrugineus* site in E. Perth (v.c. 89) (A) and I identified this as subsp. *cespitosum*.

Dr R. W. M. Corner collected a specimen on 26 June 1997 from around the edge of a bog pool, which also had *Drosera longifolia*, *Schoenus nigricans* and *Utricularia intermedia*, on Ceathramh Garbh, W. of Rhiconich (altitude 75 m), in W. Sutherland (v.c. 108) and I identified this as subsp. *cespitosum*. McVean & Ratcliffe (1962) have described a site at Loch Buine Moir, Inverpolly, W. Ross (v.c. 105) which contains *Trichophorum cespitosum* in association with other species of Dr Corner's site.

ABSENCE OF PROLIFEROUS FORMS OUTSIDE THE BRITISH ISLES

The proliferation of the spikelets ("pseudo-vivipary") in British grasses has been studied by Wycherley (1953a, b). True vivipary is the germination of seeds while still attached to the parent plant (Raven & Walters 1956). "Viviparous" grasses such as *Deschampsia cespitosa* subsp. *alpina*, *Festuca vivipara* and *Poa alpina* may be glacial relics. According to Jermy *et al.* (1982), there is no record of vivipary in *Carex*.

I found no record of proliferous *T. cespitosum*, with the exception of records of two sites in E. Ross (v.c. 106) (Duncan 1980), evidently referring to proliferous subsp. *germanicum*. According to Professor A. Skogen (Bergen) (pers. comm., 1993 and 1995), "vivipary" in *T. cespitosum* is very rare in Norway. He has seen it only two or three times in the field, and these were stems hanging into wet depressions so that submersion was probably the cause [i.e. possibly true vivipary, rather than floral proliferation, G.A.S.]; all belonged to subsp. *germanicum*. Professor H. C. Prentice (Lund) (pers. comm., 1993) stated that proliferous *Trichophorum cespitosum* was unknown to her and to botanical colleagues (T. Karlsson and J. T. Johansson) in Sweden. Professor H. J. B. Birks (Bergen), (pers. comm., 1995) stated that he had seen the proliferous hybrid only twice, both times in mainland Scotland - in the Cairngorms in 1967 and in Caenlochan Glen in 1976. I have been unable to find a specimen of a proliferous form from outside the British Isles, despite looking through the sheets of *T. cespitosum* in B, M, W and WU.

Festuca vivipara requires a wet climate to enable its propagules to root, so is particularly common in N. W. Scotland. Perhaps the same is (or has been) true of the proliferous *Trichophorum* hybrid and especially proliferous subsp. *germanicum*.

DISTRIBUTION IN GERMANY, HOLLAND AND BELGIUM

Although subsp. *germanicum* is the common and widespread plant in Germany, it is not the only subspecies to occur there. Specimens exist of subsp. *cespitosum* from areas above c. 600 m between Munich and the Zugspitze, such as Oberammergau (BM) and near the Starnberger See and Bad Tölz (M). This subspecies also occurs at low altitude in Prussia and Schleswig-Holstein in the north of Germany. There are specimens (K) from around 1900 from near Königsberg (now Kaliningrad, in Russia), from raised mires, 4 m above sea-level, with *Eriophorum vaginatum*, *Rhynchospora alba*, *Drosera rotundifolia*, *Empetrum nigrum*, *Calluna vulgaris*, *Scheuchzeria palustris* and *Sphagnum* sp.

However, it was Foerster's short paper in 1963 (in which he believed he had found subsp. *cespitosum* growing with subsp. *germanicum* in the Hohes Venn) which led to Oberdorfer's extensive work in Schwarzwald and Vosges. Paradoxically, Foerster's supposed subsp. *cespitosum* from the Pannenstertz proved to be the hybrid, as I had already correctly guessed (see section of the present paper, Identification, Fruiting). Nevertheless there is in M a specimen of subsp. *cespitosum*, which Foerster collected in 1964 in the Hohes Venn, but apparently in a different locality, and also one which he collected in Schwarzwald.

Oberdorfer (1969) described various habitats for subsp. *cespitosum*, including flushes and raised mires and one at 1000 m altitude in the Hornisgrinde region of Schwarzwald, where subsp. *germanicum* and subsp. *cespitosum* grew side by side, although sharply separated, the latter in wet depressions in the eroded peat (like subsp. *germanicum* and the hybrid in Northumberland). Oberdorfer's identification of subsp. *cespitosum* was evidently based almost entirely on the sheath-opening/blade length character and Fig. 1 in the present paper shows quite appreciable overlap between subsp. *cespitosum* and the hybrid. He does not mention substomatal cavities or fruiting and I have found no voucher specimen. It is therefore likely that at least some of his records for subsp. *cespitosum* could have represented the hybrid.

Through Dr W. Lippert I received from Dr. E. Foerster a copy of a paper which the latter had apparently never completed.

In this paper Foerster stated that in 1969 R. Tüxen had sent him specimens from moors of the Oberharz, of a plant not identifiable as either subsp. *germanicum* or subsp. *cespitosum*, using the key in Foerster (1963), so in 1970 Foerster visited the Oberharz. He found that on moors, on wet paths, and above all in the *Molinia caerulea* phase of the moor, subsp. *germanicum* occurred, but on the intact moor surface there was a population in which the stem anatomy was that of subsp. *cespitosum*, but in which those characters which are recognisable macroscopically were apparently intermediate between those of subsp. *germanicum* and subsp. *cespitosum*. These plants were abundant and often developed in ring-form and with a diameter sometimes well over 1 m. This indicates a very slow or quite stagnant growth of the mire over a long period (standstill complex), or an extraordinarily great age of the individual. In the following year he also found similar plants in the low country of N. W. Germany and in other German highlands.

The occurrence of subsp. *cespitosum* has been claimed in the Netherlands by Kern *et al.* (1947) and Reichgelt (1956). In his paper, Foerster reported that he had investigated the voucher specimens in L on which this occurrence was based and that, according to their macroscopically recognisable characters, they belonged to the same "tribe" as the plants from Harz. He proposed to publish this as a new subspecies: *Trichophorum cespitosum* (L.) Hartman subsp. *hercynicum* subsp. nov.

Foerster's manuscript contains excellent drawings showing the sheath/blade character and stem cross-sections and gives depths of the substomatal cavities in subsp. *germanicum*, *cespitosum* and *hercynicum*. These all agree quite well with those from the corresponding material from Northumberland, the hybrid from the latter corresponding to subsp. *hercynicum*. Surprisingly, there is nothing in his manuscript to suggest that he thought subsp. *hercynicum* might be a hybrid of the other two subspecies, or that it failed to fruit.

I propose that this hybrid be named *Trichophorum cespitosum* nothosubsp. *foersteri*, in view of the plant having been found by E. Foerster in the Harz Mountains.

Although not mentioned by Foerster, the occurrence of subsp. *cespitosum* has been claimed by Dumont (1976) in Haute Ardenne in Belgium, who states "An unequivocal identification in the field requires only an examination of the uppermost leaf and a comparison between the lamina length and the length of the sheath opening". However, in my opinion, this is quite insufficient and Dumont's illustrations of stem cross-section represent the hybrid, rather than subsp. *cespitosum*. The description of habitat given is very similar to that of the hybrid in the Border Mires.

Trichophorum cespitosum (L.) Hartman

Synonymy

Scirpus cespitosus L.

KEY TO TAXA (FOR NON-PROLIFEROUS PLANTS)

1. Sheath-opening ≥ 2 mm; length of sheath-opening/blade length > 0.4 ; fruit produced subsp. *germanicum*
- 1a. Sheath-opening ≤ 2 mm; length of sheath-opening/blade length ≤ 0.4 ; fruit produced or not 2
2. Sheath-opening ≤ 1 mm (its margin without red colour); length of sheath-opening/blade length < 0.25 ; fruit produced subsp. *cespitosum*
- 2a. Sheath-opening 1–2 mm (its margin possibly red-dotted); length of sheath-opening/blade length < 0.4 ; fruit not produced nothosubsp. *foersteri*

It seems that two taxa of *Trichophorum* sometimes become interwoven in the same tuft of *Trichophorum* and this can lead to confusion in identification.

SUBSPECIES

a) subsp. *cespitosum*

Synonymy

T. austriacum Palla, *T. cespitosum* subsp. *austriacum* (Palla) Hegi, *S. cespitosus* subsp. *cespitosus*, *S. cespitosus* var. *callosus* Bigelow

Description: opening in upper sheath suborbicular, 1 mm in diameter, with blade 5–10 \times as long as opening (length of sheath-opening/blade length < 0.25); plant fruiting; aerenchyma absent; substomatal cavities 20–26 μm deep.

Distribution: Arctic-Alpine

b) subsp. *germanicum* (Palla) Hegi

Synonymy

T. germanicum Palla, *S. cespitosus* subsp. *germanicum* (Palla) Broddeson, *S. germanicum* (Palla) Lindman

Description: opening in upper sheath oblique, 2–3(–5) mm long and 1 mm broad, with blade up to 2 \times as long as opening (length of sheath-opening/blade length > 0.4); plant fruiting; aerenchyma present; substomatal cavities 6–7 μm deep.

Distribution: Atlantic-Subatlantic

Trichophorum cespitosum* (L.) Hartman subsp. *cespitosum* \times subsp. *germanicum* (Palla) Hegi = nothosubsp. *foersteri* G. A. Swan, nothosubsp. *nov.

Per rationem foraminis vaginae contra longitudinem laminae foliae 0.2–0.35, cavernulae stomatis profunditate 8–18 μm , fructu sterili parentibus subsp. *cespitoso* (ratio < 0.25 , cavernulae profunditas 20–26 μm , fertilis) et subsp. *germanico* (ratio > 0.4 , cavernulae profunditas 6–7 μm , fertilis) differt.

Differing in the ratio of length of sheath-opening to length of blade 0.2–0.35, the depth of the substomatal cavities 8–18 μm , and sterile fruit, which in subsp. *cespitosum* are ratio < 0.25 , cavities 20–26 μm deep, fertile and in subsp. *germanicum* are ratio > 0.4 , cavities 6–7 μm deep, fertile.

HOLOTYPE: S. Northumberland, v.c. 67, Gowany Knowe Moss (NY/727.787), raised mire, 20 July 1996, G. A. Swan (BM).

SUMMARY

The hybrid is the predominant plant of raised mires, not only in Northumberland, but also in the Harz Mountains in Germany; it occurs also in S. W. Germany, Holland, Belgium and Norway, as well as elsewhere in Britain and Ireland. In earlier times, subsp. *cespitosum* presumably covered areas which the hybrid does today. The survival of the sterile hybrid is reminiscent of that of *Circaea* × *intermedia* (Raven 1963) and *Nuphar* × *spenneriana* (Heslop-Harrison 1953).

Many records for subsp. *cespitosum* represent this hybrid, so populations of *T. cespitosum* in these areas should be re-examined. A plant which has a sheath-opening c. 1 mm and which is producing mature fruits in short, broad heads is likely to be subsp. *cespitosum*. A plant with a sheath-opening 1–1.5 mm and in which the top of the stem becomes more or less bare by July is likely to be the hybrid. In either case, the identification should be confirmed by microscopic examination of the stem-section.

Although subsp. *cespitosum* does not in general require base-rich conditions, in regions where subsp. *germanicum* is also present, subsp. *cespitosum* may be found only in base-rich areas because only there has it escaped hybridisation; attempts should be made to find out whether or not this statement is generally true.

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