COMMENTS ON SPHAGNUM CAPILLACEUM

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It is difficult to believe that one of the most common peatmosses of North America and Eurasia has been in nomenclatural confusion for more than two centuries. After 200 years of discussion and debate, bibliographic and legalistic, a solution seems possible, and an easy one, at that. The species in question is generally known in North America as Sphagnum capillaceum (Weiss) Schrank, but in Europe, and recently on this side of the water too, the name S. nemoreum Scop. has received considerable favor; Sphagnum capillifolium (Ehrh.) Hedw. and S. acutifolium Ehrh. ex Schrad. are in less common use. All these names originated in the 1700's—S. nemoreum dates back to 1772, S. capillifolium to 1782, S. capillaceum to 1789, and S. acutifolium to 1794. The last three can be traced back even further, to Dillenius and Linnaeus, by references to synonymy at a lower rank.

The oldest name at the level of species is undeniably S. nemoreum, but its application is by no means certain. The meaning of the others is made patent by references in their protologues. In fact, the specimen in Dillenius' herbarium already designated as the type of S. capillaceum (Taylor, 1953) could serve as the lectotype for all three. Therefore, only S. nemoreum remains in need of definition and typification. Andrews (1959) conceded that the name S. nemoreum Scop. is older than S. capillaceum or S. acutifolium but pointed out that its "description is not adequate for identification, and as far I am aware no material of it has been preserved. Evidence as to its identity adduced by S. O. Lindberg and K. F. Dusén is highly circumstantial and unconvincing. . . . On the other hand the name capillaceum rests at least in part on specimens preserved in the Dillenian herbarium, and Miss Jane Taylor of the Kew Herbarium . . . took the trouble to look up the Dillenian specimens." Andrews did not take into consideration the nomenclatural worth of S. capillifolium.

The history of confusion concerning all these names, so well documented in the literature, is reviewed in interesting detail by Isoviita (1966). He considered the name S. capillifolium "valid, legitimate, and usable" and went on to explain that "its lectotype is the same as that of S. capillaceum. Since it is older than the latter, it would have to be adopted if the name S. nemoreum is rejected.... It would be very desirable, however, to preserve this old name [that is, S. nemoreum] in its present sense. But the justification of its use can be proven only by studies made at the type locality, and even then they would scarcely be of binding significance." S. acutifolium can be eliminated from consideration because of its relatively late appearance and because Schrader, on originating the name, referred to its synonymy Linnaeus S. palustre var. β and thus included in his concept the original material of S. capillifolium and S. capillaceum as well! It is thus an illegal name.

In the absence of original material, one could give definition to S. nemoreum by designating a neotype. This means, in effect, conserving that epithet over one which is nomenclaturally acceptable. Isoviita favored the retention of S. nemoreum because that is the name sanctioned by usage in Fennoscandia (where much of the literature on Sphagnum originated.) For similar reasons based on American tradition, I like S.

capillaceum better. That is the name which Andrews used in his revision of the North American species (1913) and throughout his long career as the world's leading sphagnologist and the name which appears in most of the checklists, manuals, and floristic catalogues made available to American students. However, following Isoviita's own arguments and conclusions, I believe the best and only logical choice to be S. capillifolium. Such a choice necessitates nomenclatural changes regarding two entities which I have already treated as varieties of S. capillaceum (Crum, 1971, 1973):

Sphagnum capillifolium var. tenellum (Schimp.) n. comb.

- S. acutifolium var. tenellum Schimp., Mém. Hist. Nat. Sphaignes 63. 1857. S. rubellum Wils., Bryol. Brit. 19. 1855.
- S. capillifolium var. tenerum (Sull. & Lesq. ex Sull.) n. comb.
- S. tenerum Sull. & Lesq. ex Sull. in Gray, Man. Bot. No. U.S. (ed.2). 611. 1856.
- S. evansii Warnst., Hedwigia 47: 100. 1907.
- S. eatonii Warnst., Ibid.
- S. nemoreum var. tenerum (Sull. & Lesq. ex Sull.) Nyh., Illus. Moss Fl. Fennoscandia 2: 725. 1969.
- S. capillaceum var. tenerum (Sull. & Lesq. ex Sull.) Crum, Bryol. 74: 168. 1971.

The varieties of S. capillifolium—the var. tenellum, the var. capillifolium, and the var. tenerum-provide (in that order) an elegant example of the tendency for stem leaves to vary in the direction of branch leaves in shape and structure. Varying degrees of "hemi-isophylly" are found in several of the species and species-complexes of Sphagnum and have helped to give that genus a reputation for difficulty. Like many other kinds of variation in Sphagnum, isophylly can be related to differences in habitat, such as seasonal fluctuations in wetness (see Jensen, 1883; Åberg, 1937; Agnew, 1958; Mägdefrau & Winkler, 1966; Jelenc, 1970; Rahman, 1973). At their best and most typical expressions the various members of the S. capillifolium complex are easy to recognize by microscopic means, but they intergrade in such a way that they can sometimes be sorted out only by arbitrary decisions. While I grant that these are matters subject to individual interpretation, I find it convenient to recognize the differences, such as they are, at a low taxonomic level until it can be determined whether they are genetically meaningful or not. Environmental influences causing such variation are difficult to detect and analyze, because no dependable aspect differences can be spotted in the field.

The distinguishing features of the var. capillifolium are found in its oblong-ovate, involute-pointed stem leaves. The border is usually not much broadened at base. The hyaline cells are fibrillose on the outer surface and mostly resorbed on the inner. Large, rounded membrane gaps are often found on the outer surface of some cells. The var. tenerum has stem leaves more concave and pointed, with a lesser development of the basal border and with hyaline cells showing an abundance of elliptic pores along the commissures on the outer surface. The var. tenellum has flat, lingulate stem leaves with a broad apex and a well-marked, broad basal border. There are no pores or membrane gaps, and fibrils are generally lacking or reduced, but membrane pleats are well represented in the hyaline cells of stem leaves.

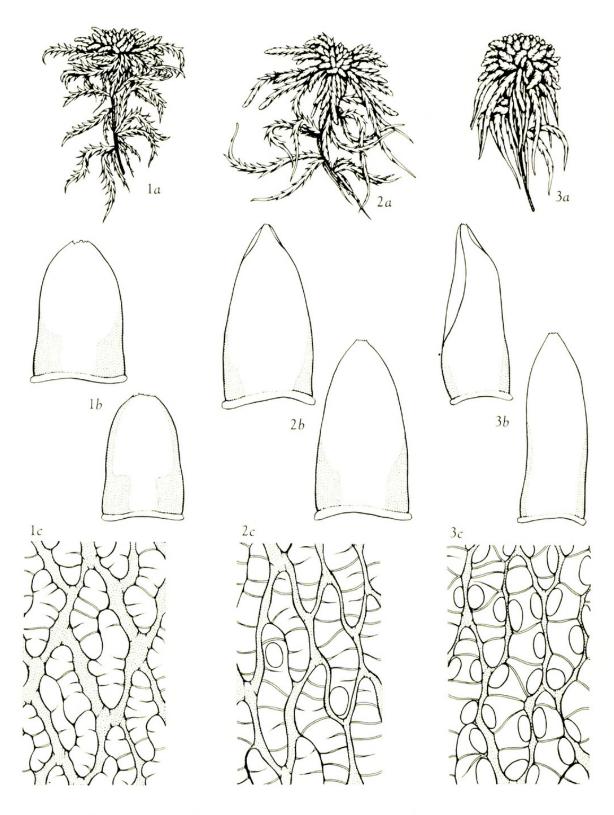
Were it not for the fact that the var. tenellum is so characteristic of the particularly oligotrophic and acid conditions of raised and blanket bogs in western Europe and other regions of high humidity (and often given the dignity of species rank, as S. rubellum), I would view it even more parsimoniously. In North America it is not at all restricted to oceanic climates or, as far as I have been able to determine, any particular environmental niche. In the continental interior and more commonly perhaps northward in the boreal forest, it is common and widespread on hummocks in both rich and poor fens. The habitat requirements need to be more intensively explored. I

think of the var. tenellum as occupying more elevated portions of hummocks and thus more acid-loving than the var. capillifolium, which however has a broad tolerance to conditions of pH and acts as a hummock former in the hollows and also occurs commonly in more acid conditions at the sides and tops of hummocks. Andrews once told me that he found the var. tenellum less distinctive here than in Europe. He stated in print (1959) that the variety should be recognized at some level even though intergrades make it impossible to separate some specimens except by arbitrary choice. It seems to be significant that Osvald (1940) also, with a background of extensive field work in Europe and in North America, found differences between the typical variety and the var. tenellum less impressive here than in Europe. At least in his North American studies, he considered them mere transitional forms.

The var. tenerum was previously considered essentially limited to the Coastal Plain in eastern North America. Andrews (1913) treated it at the specific level, but later (1959) characterized it as unsatisfactory species at best, ranging along the coast from Newfoundland to Alabama and inland to Tennessee. "Difficulty in identification rests especially upon the difficulty of giving a readily tangible diagnostic character. I have been obliged to limit the points of difference to the obese branches with very imbricate leaves which show an especially lax areolation with the empty cells (leucocysts) showing very strong convexity on the dorsal surface. This I will freely admit is not very satisfactory and while for the present disposed to maintain the species, I have no quarrel with anyone preferring to regard it as a variety of S. capillaceum and can at any rate understand the contention that it should be merged in this 'species." He had seen no material from Europe that was correctly named and thought that European records could be traced to a misunderstanding. He referred to this misunderstanding most specifically (and with irritation) in reference to Mrs. Lange's report from Denmark (1955). Andrews' valuable paper of 1933 presents further nomenclatural information of interest, on this taxon and also on a misuse of the name S. tenerum for something that he referred "rightly or wrongly" to S. meridense (Hampe) C. M. Elsa Nyholm (1969) included the taxon, as S. nemoreum var. tenerum (Sull. & Lesq.) Nyh., in the flora of Fennoscandia. Rønning (1958) preferred to consider it a modification of S. nemoreum, and Isoviita, in accounting for all the Sphagna of Europe (1966), said, "Like Ronning, I myself admit that my acquaintance with this species is deficient and is confined merely to herbarium specimens. If it were not for the fact that Andrews, well known for his broad concept of species, considered S. tenerum to be a distinct species, I would be willing to add this name to the synonym list of S. nemoreum."

Contrary to previous opinions, according to my understanding and definition, the taxon—whether species of variety—does indeed occur in northern and central Europe. I choose to call it S. capillifolium var. tenerum. I have seen specimens from the Caucasus and Japan. It is not uncommon in the interior of North America, ranging in fact across the continent, but it is most characteristic of the Atlantic Coastal Plain. It is variable in growth form and appearance, as well as in structure, but I have little trouble in recognizing it microscopically. As far as I have been able to determine it shows little or no selectivity as to habitat, apparently occupying the same kinds of niches as the var. capillifolium, at least in inland localities.

The accompanying illustrations, prepared by Constance Butley, show the three epxressions of S. capillifolium, in their most distinctive forms but not the intergrades which make identification so difficult. The form of the capitulum, the shape of the stem leaf, and the degree of isophylly demonstrated by the stem leaf structure present a striking contrast at the extremes. Whether the differences vary with habitat conditions or whether they represent phylogenetic trends can scarcely be determined by sorting specimens or by casual observation in the field.



The Sphagnum capillifolium complex consisting of three intergrading forms shown here in their most distinctive expressions. Var. tenellum. 1a. Capitulum, \times 2. 1b. Stem leaves, \times 27. 1c. Cells of upper median portion of stem leaf, outer surface, \times 400. Var. capillifolium. 2a. Capitulum, \times 2. 2b. Stem leaves, \times 27. 2c. Cells of upper median portion of stem leaf, outer surface, \times 400. Var. tenerum. 3a. Capitulum, \times 2. 3b. Stem leaves, \times 27. 3c. Cells of upper median portion of stem leaf, outer surface, \times 400.

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