

Notes on Fissidens. I and II

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ABSTRACT

In Note I it is shown that the delimitation of the sections *Bryoidium*, *Pachylomidium*, *Aloma* and *Semilimbidium* subsect. *Bryolimbidium* is very vague. Consequently they are united. The resulting section contains the type species of the genus *Fissidens* and the correct name for it is, therefore, *Fissidens*.

In Note II *F. bambergerei* Schimp. ex Milde, *F. firmus* Linb. ex Roth, *F. herzogii* Ruthe in Herzog, *F. canariensis* Bryhn and *F. bilewskyi* Pot. Varde are reduced to synonymy under *F. minutulus* Sull. *F. minutulus* is described, figured and characterized. Besides, it is compared with *F. ovatifolius* Ruthe.

F. pusillus (Wils.) Milde, *F. minutulus* Sull. and *F. viridulus* (Swartz) Wahl. are compared and found to be three distinct species. *F. subimmarginatus* Phil. is reduced to synonymy under *F. exiguus* Sull.

I. ON THE ARBITRARY NATURE OF THE DIVISION IN SECTIONS OF THE GENUS FISSIDENS.

THE SECTIONS ALOMA (KINDB.) C. MUELL., BRYOIDIUM C. MUELL., FISSIDENS HEDW., PACHYLOMIDIUM C. MUELL. AND SEMILIMBIDIUM C. MUELL. SUBSECT. BRYOLIMBIDIUM NORK. IN GANG.

In my first paper on *Pachylomidium* (Bruggeman-Nannenga, 1973) I stated my intention to deal in more detail with the transitions between that section and some others in a later paper.

I had planned to do so after having concluded my revision of the section *Pachylomidium*. This procedure would have had certain advantages. For

one thing I would by then probably have been able to incorporate several more transitional species in the discussion. Secondly, it would then no longer have been necessary to explain why, after having shown that there is no reason to maintain *Pachylomidium* as a separate section, I still go on revising it. I will try to justify this in a further paper on the section *Pachylomidium*.

THE SECTION BRYOIDIUM AND THE SECTION PACHYLOMIDIUM

According to Brothrus (1924) these two sections can be separated by the thickness of the border of the leaves and by the ecology. Species of *Pachylomidium* are supposed to have a pluristratose border and to grow in aquatic habitats, whereas those of *Bryoidium* are said to have a unistratose border and to grow terrestrial.

Several authors (Demaret, 1959; Melnichuk, 1960) reported some *Bryoidium* species as having a pluristratose border. Other authors (Bizot & Pierrot, 1963; Lambinon, 1968 and Norkett, 1969) found that the border of several species may be unistratose as well as pluristratose.

The difference in ecology too is not stable enough to warrant a separation of both sections. For instance *F. pusillus* (Wils.) Milde very often grows on stones in or near running water, but is also found, though growing less vigourously, in less wet places. Moreover, *F. pusillus* is one of those species in which the border may be unistratose as well as pluristratose; it is indeed an intermediate species.

Another example showing that the difference in ecology does not hold is provided by a not yet described Newguinean species which has been found in and near running water, but also outside the influence of running water.

F. rigidulus Hook. f. et Wils., too is, though it normally grows on stones in or near running water, also found in less wet habitats. More examples of species growing within the influence of streaming water as well as in dryer places are given by Norkett (1969).

The *F. bryoides* complex furnishes further proof that the boundary between *Pachylomidium* and *Bryoidium* is extremely vague. The greater part of the species of this complex have been described in *Bryoidium*. I found that several *Pachylomidium* species are linked by intermediate collections to one of its members, viz. *F. pusillus* (Wils.) Milde. For this reason these species too belong to the *F. bryoides* complex. These species are *F. appalachensis* Zand., *F. rufulus* Bruch et Schimp. in B.S.G. and *F. crassipes* Wils. ex B.S.G. I will give more details about these extensions of the *F. bryoides* complex in the papers dealing with the species involved: in a paper on the Northamerican species for *F. appalachensis* and in a paper about the European species for the other ones.

The logical conclusion from the above is that the sections *Pachylomidium* and *Bryoidium* are to be united, as has been done by several authors. Grout (1943) treated the only then known Northamerican *Pachylomidium*

species, viz. *F. "rufulus"* (= *F. ventricosus* Lesq.) as a member of the section *Bryoidium*. Norkett (in Gangulee, 1971) treated *Pachylomidium* and *Bryoidium* as subsections of the section *Fissidens*. In my opinion *Pachylomidium* and *Bryoidium* should not be retained as separate taxa of any rank as they shade into each other. The section resulting from this union should be called *Fissidens* as it contains the lectotype species of the genus, viz. *F. bryoides* Hedw.

The section *Fissidens* is characterized by leaves with smooth cells and a prosenchymatic border on all three laminae.

Even before the above mentioned "*Pachylomidium*" species were found to belong to it, the *F. bryoides* complex was rather heterogeneous from a sectional point of view. *F. pusillus* (Wils.) Milde is, as we have seen above, in all respects intermediate between "*Pachylomidium*" and "*Bryoidium*". *F. bryoides* Hedw., *F. viridulus* (Swartz) Wahl., *F. texanus* Lesq., *F. repandus* Wils. and *F. minutulus* Sull. belong to "*Bryoidium*".

The last two remaining members of the *F. bryoides* complex, *F. andersoni* Grout and *F. exiguus* Sull. have a border that is limited to the lamina vera of the best developed leaves. Besides, like the other members of this complex, they have smooth cells. Therefore, they do not fit in any section at all (see also Potier de la Varde, 1953; Bizot & Pierrot, 1964, p. 233-234).

Some authors (Ruthe, 1870 and in Limpricht, 1904; Philibert, 1884; Grout, 1943) place such species in the section *Semilimbidium*, thus neglecting the absence of papillae. Norkett (in Gangulee, 1971) followed their example and refined it by creating a non papillose subsection of *Semilimbidium*. He named this subsection *Bryolimbidium*.

According to Potier de la Varde (1931, 1944 and 1945, p. 37) only species with papillose cells should be admitted to *Semilimbidium*. Species with smooth cells and an incomplete border should in his opinion be attributed either to the section *Aloma* or to the section *Bryoidium* (now part of the section *Fissidens*). I not only agree with this last author, but also propose the sections *Fissidens* and *Aloma* to be united.

THE SECTION ALOMA AND THE SECTION FISSIDENS

The species of *Aloma* are supposed to be completely borderless; those of *Fissidens* have, according to the diagnosis, a prosenchymatic border, i.e. a border composed of elongated cells with tapering ends, on all three laminae. If a border is present on all three laminae this is known as "completely bordered", even if the border happens to be absent near the apex and near the insertion. If the border is wanting in large parts of the dorsal and apical lamina this is known as an "incomplete" or "disrupted" border.

However, the difference between *Aloma* and *Fissidens* is not as sharp as the above suggests, the transition from unbordered to completely bordered being in all respects a gradual, continuous one. Consequently

the difference bordered-unbordered is neither distinct nor essential enough to justify its use for separating the two sections.

This gradation is evident in the process of border formation. I have the impression that the sequence in which the border is formed as well as the behaviour of individual cells during this process are more or less alike in all species.

The following description of border formation is based mainly on a study of herbarium material of *F. crassipes* Wils. ex B.S.G. subsp. *philibertii* (Besch.) Walt. It has been confirmed by incidental observations on herbarium material of many "*Pachylomidium*" species, several species of other sections, field observations on *F. crassipes* subsp. *crassipes* Wils. ex B.S.G. and by a study of cultivated *F. crassipes* subsp. *crassipes*, *F. ventricosus* Lesq. and *F. rigidulus* Hook. f. et Wils. plants. The last two were kindly sent to me by respectively Mrs Dr E. Lawton and Dr B. O. van Zanten. I have not followed the differentiation of individual cells.

Border formation starts on the lamina vera. It may start in its middle or at the base, intramarginal (figs. 1a and b) or marginal. On the cellular level it starts by one or a few cells becoming slightly elongate, i.e. prosenchymatic. Gradually, more and more cells will join this process. Consequently it is impossible to draw a sharp line between an unbordered and a bordered lamina vera. Once the lamina vera has become bordered the border spreads gradually around the leaf. This extension may proceed in two ways: either it starts in the apical lamina, or it starts in both laminae at about the same time. In the apical lamina the first cells to become elongated are those at the base; in the dorsal lamina the border starts in the middle or a little above it and spreads from there towards the apex and insertion. Subsequent stages of border formation on the dorsal lamina in *F. crassipes* subsp. *philibertii* are shown in figs. 2a-d. The arrows in fig. 2c indicate the places where it is apparent that the marginal cells are still in the process of lengthwise stretching.

The vagueness of the difference bordered-unbordered is also clear from the variation in border development within some species: occasionally a species is so variable in this respect that its normal display of variation covers the whole gap between the sections *Aloma* and *Fissidens*. Such species are, for instance, *F. crassipes* subsp. *philibertii* and *F. texanus* Lesq.

In these species the following types are found: leaves with a well developed border on all three laminae (a), leaves with a well developed border on the lamina vera and either traces of a border on both the dorsal and apical lamina, or traces of a border on the dorsal lamina and a more or less well developed border on the apical lamina (b), leaves with a well developed border on the lamina vera and a more or less well developed one on the apical lamina (c), leaves with a border on the lamina vera only (d) and completely unbordered leaves (e).

1. *F. crassipes* subsp. *philibertii* (Besch.) Walt.

Although samples of this subspecies that are homogeneous with regard to the extension of the border are occasionally found, most collections are composed of a mixture of two or more of the above mentioned possibilities. A sample of this subspecies corresponding with description *a* is the collection of *F. crassipes* subsp. *philibertii* distributed as *Husnot*,

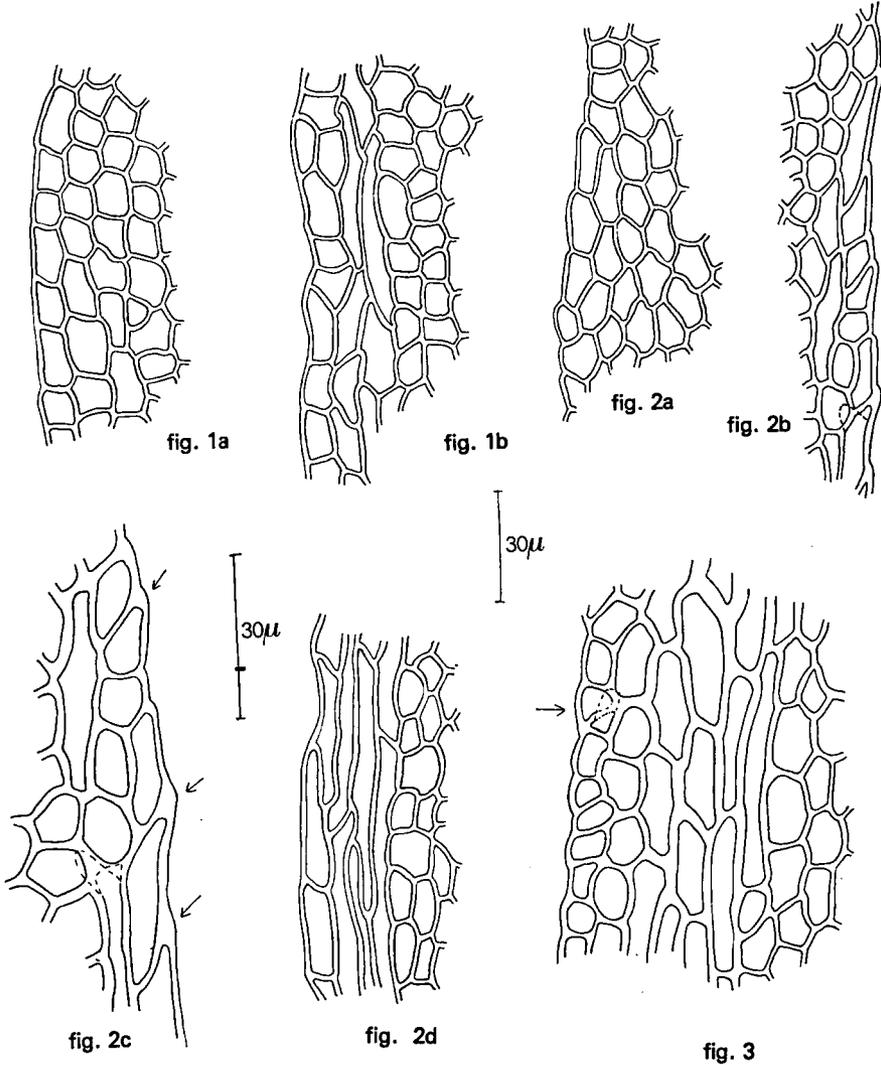


Fig. 1 and 2: *F. crassipes* subsp. *philibertii* (Besch.) Walt. (Pierrot 60-453). Fig. 1, a: unbordered margin in the middle of the lamina vera; b: margin in the middle of a lamina vera in which border development has just started. Fig. 2, a: margin of the middle of the dorsal lamina before border formation has started; b: idem with the first traces of a border appearing; c: detail of the lower part of fig. 2b showing the growing points at the tips of not full-grown border cells (arrow); d: middle part of a dorsal lamina with a distinct border. Fig. 3: traces of a border in the middle part of the lamina vera of a perichaetial leaf of *F. exilis* Hedw. (Tienstra & Veenbaas 43).

Musci Gall. 753. A mixture of *a*, *b*, *c* and *d* is found in the type collection of *F. crassipes* var. *submarginatus* Fleisch. & Warnst.

The type collections of *F. warnstorffii* Fleisch. & Warnst., *F. moureti* Corb., *F. mnevidis* Amann and *F. bambergeri* Schimp. ex Milde var. *aegypticus* Ren. & Card. are all more variable with respect to the border than was indicated in their original descriptions. In all of them a combination of *a*, *b*, *c* and *d* is found. In *F. bambergeri* var. *aegypticus* situation *a* is rare; in the other collections it is common or even prevalent. All the above mentioned types belong to synonyms of *F. crassipes* subsp. *philibertii*. In a Persian sample of this subspecies (*Schiffner* 1411) a combination of *a*, *b*, *c*, *d* and *e* is found. In the herbarium of *Thériot* (PC) I found a collection by *Le Maire*. Part of this sample has apparently been cultivated during several years. The original collection answered description *a*, *b* and *e*; the one indicated as "cult. 1927" *b* and *c* and the one indicated as "cult. 1929" *c*. Though situation *e* is common in young plants and small leaves I have never seen a sample of *F. crassipes* subsp. *philibertii* with only completely unbordered leaves.

2. *F. texanus* Lesq.

In the type collection of a synonym of *F. texanus*, viz. *F. incurvus* var. *brevifolius* Ren. & Card., situations *a*, *b*, *c* and *d* are found. This is figured in Pursell (1976: figs. 5–9). The same degree of variation is found in many other samples of this species.

Most species are, unlike the above ones, not variable enough with respect to the extension of the border to cover the whole gap between unbordered and bordered. A number of them together, however, may. The following is the description of a series of species which links the sections *Aloma* (unbordered) and *Fissidens* (bordered). The species of this series are arranged according to the maximal extension of the border known to occur in each of them, so not necessarily according to the extension of the border most commonly found.

At the one end of this series we find the typical *Aloma* species, i.e. the completely borderless ones. For examples see Potier de la Varde (1943). However, one should be prepared to find dubious places in or near the margin of the lamina vera of the best developed leaves of any species that has been reported as borderless. The next step is furnished by species like *F. exilis* Hedw. In this species a weak kind of border is (always?) found on the lamina vera of the perichaetial leaves (fig. 3).

This figure shows, besides the occurrence of elongated cells, two peculiarities which are not found, or at least less distinct in the other species. For one thing the walls of the elongated cells are distinctly thickened and secondly, the parenchymatic margin is bistratose (see arrow) in a tiny spot. A bistratose parenchymatic margin is supposed to be a diagnostic character of a part of the section *Serridium*, but it is not at all uncommon in *Aloma* species either.

A slightly better developed border is found in *F. arnoldii* Ruthe (Potier de la Varde, 1936 and 1943 plus observations by myself). In this species

a more or less conspicuous border is found on the lamina vera of the perichaetial leaves; the less well developed leaves are borderless. Next in this series comes *F. intralimbatus* Ruthe (fide Potier de la Varde, 1944), immediately followed by *F. exiguus* Sull. In both species a border may be found on the lamina vera of the perichaetial leaves as well as on that of well developed vegetative leaves. In one case I found next to the border on the lamina vera also traces of a border on the dorsal lamina of *F. exiguus* (see page 400). The next step leads to those species which often, or always, have small portions of the margin with groups of border cells on either the apical lamina alone, or on both the dorsal and apical lamina. Examples are *F. arcticus* Bryhn (fide Steere & Brassard, 1974) and *F. ranuii* Gang. (fide Gangulee, 1971). Then follow those species in which the maximal extension of the border is a complete one. Some of these, as a rule, have an incomplete or even wanting border, e.g. *F. texanus* Lesq., *F. crassipes* subsp. *philibertii* (Besch.) Walt; other ones regularly have an incomplete border, e.g. *F. crassipes* subsp. *crassipes* Wils. ex B.S.G., *F. pusillus* (Wils.) Milde and *F. minutulus* Sull. According to Roell (1911) *F. arnoldii* would belong here too. This, however, is not in accordance with my own observations. In most species in which the maximal extension of the border is a complete one, the occurrence of incompletely bordered leaves is exceptional, e.g. *F. rufulus* Bruch & Schimp. in B.S.G., *F. ventricosus* Lesq., *F. rigidulus* Hook. f. et Wils. etc.

Little is known about the factors which determine the formation of a border. At least in some species poor growth conditions seem to inhibit border development. I observed this in plants under cultivation of *F. crassipes* subsp. *crassipes*, *F. ventricosus* and *F. rigidulus*. This effect was clearest in *F. crassipes* and least distinct in *F. rigidulus*. Occasionally cultivated plants of *F. crassipes* reach a considerable length before the first traces of a border appear. In *F. ventricosus* border formation may be postponed until several leaf pairs have grown. The same holds for the formation of a border on the dorsal and apical lamina in *F. rigidulus*. In all these cases of retarded border formation the size of the leaves was abnormally small.

In the field I observed twice (sample BN 433a and b and BN 436a and b) that samples of *F. crassipes* subsp. *crassipes*, collected in the same locality but on slightly different habitats differed considerably. Samples collected in a relatively wet habitat consisted of fairly typical, completely bordered plants, whereas samples from drier habitats were somewhat atypical, being smaller, with younger sporophytes and often incompletely bordered.

In view of the above one should be wary taking into account species which are characterized by an incomplete border. Especially so when only one or two samples of such a species are known, as is the case with *F. ranuii* Gang., or when like *F. arcticus* Bryhn, it grows in a region where rather severe conditions are prevalent. Such species may very well be no more than a poor form of some bordered species: for instance *F. ranuii*

could be *F. rigidiusculus* Broth. ex Gang. and *F. arcticus* *F. minutulus* Sull.

In the above we have seen that 1) not all species of the *F. bryoides* complex are completely bordered, 2) a border is not suddenly formed, but very gradually, 3) several species vary from borderless to completely bordered, 4) a number of species has a border extension which is intermediate between unbordered and completely bordered and 5) environmental circumstances may delay the formation of a border.

All this amounts to the conclusion that the distinction between unbordered and bordered leaves, so the only difference between the sections *Aloma* and *Fissidens*, is vague and unreliable. Though he did not say so it was probably because of similar observations that Jensen (1939) treated the Norwegian species of the sections *Aloma*, *Bryoidium* and *Pachylomidium* as species of the section *Bryoidium* emend. Jens. He was not followed by later authors.

In the present paper it is shown that not only in the case of the six Norwegian species, but also on a worldwide scale, the three sections merge into each other. As the section *Bryoidium* emend. Jens. contains the type of the genus, its correct name is sectio *Fissidens*.

THE SECTION FISSIDENS AND THE SUBSECTION BRYOLIMBIDIUM (SECTION SEMILIMBIDIUM)

The subsection *Bryolimbidium* is characterized by incompletely bordered leaves with smooth cells. Therefore, it is intermediate between the section *Bryoidium* and *Aloma*, now united in the section *Fissidens* Hedw. Consequently subsection *Bryolimbidium* too is transferred to the section *Fissidens*. The other subsection of the section *Semilimbidium*, viz. subsection *Semilimbidium*, differs from the section *Fissidens* by its papillose or mammillose cells.

Fissidens sect. Fissidens Hedw., 1801. Spec. Musc.: 152; Norkett (1969): 79, in Gangulee (1971): 453 (*emend.* Nork.).

Homotypic synonyms:

Sect. *Eufissidens* C. Muell., 1848. Syn. Musc. Fr. 1: 50, *pp*, *nom. illeg.*; Mitten (1869): 585, *pp*. – *Fissidens* Hedw. IV *Eu-Fissidens* (C. Muell.) Kindb., 1897. Eur. N. Am. Bryin. 2: 166 (subgenus fide Brotherus (1901): 353), *pp*; Brotherus (1924): 145; Grout (1936A): 173. – *Fissidens* 2 *Bryoidium* C. Muell., 1900. Gen. Musc. Fr.: 54 (sectio fide Brotherus (1901): 353), *pp*; Brotherus (1924): 146; Jensen (1939): 339 (*emend.* Jens.); Grout (1943): 171; Demaret (1959): 153; Melnichuk (1960): 75; Bizot & Pierrot (1963): 84. – sect. *Terminales* Grout (*nom. illeg.*) subsect. *Limbatus* Grout, 1936. Moss Fl. N. Am. 1: 8, *pp*, *nom. illeg.*; Grout (1936A): 173. – sect. *Limbatus* (Grout) Grout, 1941. Bryologist 44: 131, *nom. illeg.* – Lectotype species: *F. bryoides* Hedw.

Heterotypic synonyms

Fissidens III *Aloma* Kindb., 1897. Eur. N. Am. Bryin. 2: 165 (subgenus fide Wijk e.a. (1962): 275), *pp.* – *Aloma* 4 *Osmundoidei* Kindb., 1897. Eur. N. Am. Bryin. 2: 166 (sectio fide Wijk e.a. (1962): 275), *pp.*: *F. exilis* Hedw. solum; *nom. illeg.*, *syn. nov.* – *Fissidens* 6 *Aloma* (Kindb.) C. Muell., 1900. Gen. Musc. Fr.: 55 (sectio fide Brotherus (1901): 357); Brotherus (1924): 149; Grout (1941): 133, (1943): 186; Potier de la Varde (1943): 25; Bizot & Pierrot (1963): 84; Norkett (1969): 81; Gangulee (1971): 456. – sect. *Terminales* Grout (*nom. illeg.*) subsect. *Aloma* (Kindb.) Grout, 1936. Moss Fl. N. Am. I: 8; Grout (1936A): 74. – Lectotype species (*nov.*): *F. exilis* Hedw.

Aloma Kindb. 1 *Camptodontii* Kindb., 1897. Eur. N. Am. Bryin. 2: 165 (sectio fide Wijk e.a. (1962): 275), *syn. nov.* – Syntype: *F. closteri* Aust. and *F. pauperculus* How. Both are unknown to me; Brotherus (1924) and Grout (1943) treat them in the section *Aloma*. Assuming this to be correct I have reduced the section *Camptodontii* to a synonym of the section *Fissidens*.

Fissidens 4 *Pachylomidium* C. Muell., 1900. Gen. Musc. Fr.: 54 (sectio fide Brotherus (1901): 354); Brotherus (1924): 146; Demaret (159): 153; Bruggeman-Nannenga (1974): 146. – sect. *Fissidens* subsect. *Pachylomidium* (C. Muell.) Nork. in Gang., 1971. Moss. East. India adj. reg. 2: 454. – Lectotype species (*nov.*): *F. rufulus* Bruch & Schimp. in B.S.G.

Conomitrium Mont. 3 *Limbidium* C. Muell., 1900. Gen. Musc. Fr.: 71 (sectio fide Wijk e.a. (1959): 499), *syn. nov.* – Type species: *F. smaragdinus* (Lor. & C. Muell.) Broth.

Conomitrium Mont. 7 *Bryodiopsis* C. Muell., 1900. Gen. Musc. Fr.: 74 (*Conomitrium* sect. *Bryodiopsis* fide Brotherus (1901): 353; *Conomitrium* sect. *Bryodiopsis*=*Fissidens* sect. *Bryoidium* C. Muell. fide Brotherus (1901): 353). – Syntype consisting of 7 species, including several nomina nuda.

Sect. *Semilimbidium* C. Muell. subsect. *Bryolimbidium* Nork. in Gang., 1971. Moss. East. India adj. reg. 2: 455. – Type species: *F. bilaspurensis* Gang. – *syn. nov.*

Description of the section *Fissidens*

Species small to rather large, growing in a wide variety of habitats and on many kinds of substrates. Leaf margin either unbordered and entire or crenulate, or incompletely respectively completely bordered with a row of prosenchymatic cells. Cells medium sized (most cells 9–11 μm long), less often small (7–9 μm long) or large (size variable, but many cells reaching or even exceeding a length of 15 μm). Cell walls smooth. Cells, especially in species with small cells, occasionally seemingly or truly mammillose. Capsule mostly terminal, often but not always with stomata.

According to Brotherus (1924) the filaments of the peristomium teeth are spirally thickened, but see below.

MUELLER (1973) made with help of scanning electron micrographs a more exact description of the structure of the filaments of the peristomium teeth of *F. minutulus* Sull. (see MUELLER, 1973: 17, pl. 4D and 12A). The structure of the filaments turns out to be rather complicated, giving the impression of spirals when studied under a light microscope. Possibly the filaments of other species of the section *Fissidens* are structured in a similar wise.

II. REMARKS ON SOME SPECIES OF THE FISSIDENS BRYOIDES COMPLEX

A. FIVE NEW SYNONYMS TO FISSIDENS MINUTULUS SULL

F. minutulus Sull., 1846. *Musc. Allegh.*: 44; Sullivant (1864): 37, *T. 24*; non Braithwaite (1887): 81. – Type: *Sullivant* *Musc. Allegh.* 183 (FH, herb. Sullivant (holo-)). – *F. limbatus* Sull., 1856. *Rep. Expl. Surv. Railr. R. Bot.* 4 (5): 185, *f. 1*; Schofield (1969): 132, 133 Mueller (1973): 1–34, *pl. 1–35*. – Type: found near San Francisco (not seen). – *F. bambergeri* Schimp. ex Milde, 1864. *Bot. Zeit.* 22 (Beibl.): 12. – Type: *Rabenhorst* *Bryoth. Eur.* 656 (BR). – *syn. nov.* – *F. firmus* Lindb. ex Roth, 1904. *Eur. Laubm. I*: 563, *T. LII, f. 3*. – Type: *Henriques*, Coimbra, Portugal (S (iso-) ;holotype in H (herb. Lindb.) not seen). – *syn. nov.* – *F. herzogii* Ruthe in Herzog, 1905. *Ber. Zuer. Bot. Ges.* 15: 58; Potier de la Varde (1931A): 161, *f. 1–13*; Allorge (1958): 188. – Type: *Herzog*, Sardinia, Monte Albo (PC). – *syn. nov.* – *F. canariensis* Bryhn, 1908. *K. Norsk. Vid. Selsk. Skrift.* 1908 (8): 15; Persson (1938): 148; Giacomini (1939): 284. – Type: *Bryhn*, Tenerife, Las Mercedes (OSLO). – *syn. nov.* – *F. bilewskyi* Pot. Varde, 1956. *Rev. Bryol. Lich.* 25: 122, *f. 1–21*. – Type: *Bilewsky* 1011 (PC). – *syn. nov.* – Fig. 4a-h.

F. minutulus Sull. is very variable and therefore hard to characterize. Fortunately, *F. minutulus* is the only bordered species with small cells and a thin border in most of its area. However, in Florida it could be confused with *F. repandus* Wils. This species is of about the same size and also has small cells and a border. I have seen the type collection and a few other samples of *F. repandus*. Like *F. minutulus* this species is variable and therefore I find it impossible to tell whether the two are distinct species, or, if so, by which features they can be separated.

In Europe *F. minutulus* might be confused with *F. ovatifolius* Ruthe. These two can be distinguished by the dorsal lamina. That of *F. ovatifolius* either ends far above the insertion, or is, in its lower part, reduced to a narrow zone of border cells (fig. 5); that of *F. minutulus* reaches the insertion.

Plants 1–7 mm long, with up to 15 leaf pairs. *Leaves* elliptical, less often oblong, ovate or obovate; 0.5–2.0 mm long and 0.15–0.6 mm wide, ratio L/W 2–5 (6). Apex in large plants mostly acuminate or acuminately mucronate; in small plants mostly acute to indistinctly acuminate. Border

(0) 4.5–18 μm wide, as a rule nearly or completely reaching the apex, sometimes there fusing with the nerve; in small plants, however, border often ending rather far below the apex, or even, in other than perichaetial leaves, absent except for on the lamina vera. Border reaching the insertion or not. Cells small: (4.5) 6–9 (12) μm long and (3) 4.5–6 (7) μm wide, often bulging from the leaf surface. *Fertile plants*: Archegonia mostly terminal, 200–380 (480) μm long. Perichaetial leaves 0.8–2.5 (2.9) mm long and 0.15–0.6 mm wide; ratio L/W 3–9. Antheridia either in axillary buds or terminal. This may be terminal on plants of normal length, on dwarf male plants or on axillary stems. Antheridia 150–240 μm long. *Sporophyte*: seta 1.5–6 (12) mm long, capsule erect, slightly oblique or curved, peristomium teeth 21–55.5 μm wide, spores 7.5–18 μm .

Distribution: South-eastern and south-western Canada, the central and eastern part of the U.S.A. and west of the Rockies; western Europe, the mediterranean area and the Atlantic African islands.

Examined material: CANADA, BRITISH COLUMBIA: *Macoun* Canadian Musci 618 (as *F. incurvus*) (YU), 619 (as *F. incurvus* var. *viridulus*) (YU), Comox (S); *Macoun?*, Vancouver Island (FH, S); *Schofield* 22785 (C), 28508 (U). ONTARIO: *Macoun* Canadian Musci 50 (as *F. incurvus*) (YU), 60 (as *F. pusillus*) (MANCH), 100 (FH), 452 (FH), Ottawa (S); *Hand* 720 (L). U.S.A., CALIFORNIA: *Allen*, Pasadena (YU); *Bolander*, Oakland (YU); *Drouet & Groesbeck*, Tule River (NY); *Grout*, North Am. Musci Perf. 232 (YU), 297 (as *F. incurvus*) (YU); *Holzinger* 7241 (L), Musci acroc. Bor.-Am. 356 (YU); *Kingman*, Oak Knoll Canyon (YU); *Renauld & Cardot* Musci Am. septentr. exs. 208 (as *F. bryoides*) (YU). FLORIDA: *Anderson* 5271 (S). ILLINOIS: *Bruggeman-Nannenga* 1271. MARYLAND: *Fitzgerald?*, Baltimore (FH). MINNESOTA: *Holzinger* Musci Acr. Bor.-Am. 105 (YU, FH), 105B (YU, FH); *Renauld & Cardot* Musci Am. Septentr. Exs. 159C (YU, FH); *Vasa*, Minnesota (BR). MISSOURI: *Redfearn* 3387 (FH), 28604 (U). NEBRASKA: *Wolfe*, Weeping water (FH). NEW YORK: *Clinton?*, (FH). NORTH CAROLINA: *Hermann* 15273 (FH). OHIO: *Sullivant* Musci Allegh. 183 (FH); *Brooke*, Springfield (MANCH). OREGON: *Howell*, Multnoma (YU), Oregon (FH). PENNSYLVANIA: *James*, W. Schuylkill (several samples from several places and dates) (FH), Wisahickon *pp* (FH), Samantown *pp* (FH), Holmesberg (FH); *Sullivan & Lesqueroux* Musci Bor.-Am. ed. 2, 104 (as *F. incurvus*) *pp* (YU). TENNESSEE: *Morrison*, Knox Co. (FH). WASHINGTON: *Holzinger* Musci Acr. Bor.-Am. 279 (YU), 408 (as *F. incurvus*) (YU); *Piper?* Musci Occ.-Am. 42 (YU), 152 (YU). OLD WORLD, AUSTRIA: *Bauer* Musci Eur. exs. 287 (as *F. pusillus*) (MANCH); *Conard*, Krieglach (FH). BELGIUM: *Gradstein*, Warche (U). CANARY ISLANDS: *Bryhn*, Las Mercedes (OSLO); *Friedländer*, Las Mercedes (S); *Störmer*, Las Mercedes (PC, S). CAPE VERDE ISLANDS: *Chevalier*, S. Antão (PC). FRANCE: *Allorge* 115 (PC), Roumé (PC); *Amann*, Estérel (S); *Bruggeman-Nannenga* 427; *Camus*, Ile Brenat (PC); *Corbière*, Cherboung (MANCH); *Debon*, Estérel (PC); *Dismier*, Estérel (PC), Croix des Gardes (PC); *Lebel*, Manche (PC); *Pierrot*, St. Julien (PC). GREAT BRITAIN: *Bagnath*, Lye Green (MANCH); *Curnow*, Penzance, *pp* (MANCH); *Hill*, between McIplashe and Loscombe (herb. A. J. E. Smith); *Whitehead*, Marple oct. 1880 (MANCH). GREECE, CRETE: *Düll* 108 (my own herbarium); *Gradstein & Smittenberg* 1070 (U), 1222 (U). CORFU: *Hararas*, Corfu (U). IRAN: *Treĵukoo*, Ladjim (S). ISRAEL: *Bilewsky* 1011 (PC). ITALY: *Levier*, Florence (S); *Herzog*, Monte Albo (PC); *Rabenhorst* Bryoth. Eur. 656 (BR); *Reinhard*, Sardinia (S). MADEIRA: *Da Costa*, Moniz (PC), Santa (PC). MALTA: *Kramer & Westra* 4517B (U). PORTUGAL: *Allorge*, Bussaco (PC). SPAIN: *Allorge* 94 (PC).

Aberrant samples are: 1) *Grout*, North Am. Musci Perf. 309 (as *F. ventricosus*) (NY, YU, USNM, S). These plants are in all respects very large, and 2) *Allorge*, Bussaco (PC). These plants approach *F. ovatifolius* by the leaf shape.

NB The above mentioned material from YU, BR and C and part of that from PC has not been annotated because it was no longer available.

Ecology: Large plants (length of female plants 2–7 (10) mm; see also Remark 1) mostly grow on banks of brooks, gullies and roads, or on sandy or loamy soil in shady places; small plants (female plants 1.5–3 mm) usually grow on rocks in humid shady places; also on rocks in running water.

REMARK 1: many plants from the central and eastern part of North America (from North Carolina and Tennessee northward to Ontario and from the Atlantic coast to Missouri, Nebraska and Minnesota) and a few rare European samples are smaller than most samples from other parts of the area (figs. 4a and b). Such plants as a rule have a less wide and less far extended border, smaller vegetative and perichaetial leaves, a shorter seta, a smaller capsule and less wide peristome teeth. Moreover, they usually grow on rocks and never have axillary antheridia, whereas most larger plants grow on soil and often have axillary antheridia. The present study does not enable me to decide whether the cause of the above mentioned differences is ecological and/or climatological and/or genetical. As I found an overlap for all differences (morphological, ecological and geographical), I have not described the large and the small form as separate taxa.

Large plants are known as *F. herzogii* in Europe and as *F. limbatus* in North America; small plants are known under many names.

REMARK 2: the type of *F. bambergeri* consists mainly of small incompletely bordered plants in which the dorsal lamina ends far above the insertion (fig. 4c). Mixed with these are a few plants in which the lowermost leaves are as described above, whereas in the uppermost ones length and width are notably larger, the dorsal lamina reaches the insertion and the border is complete. These leaves are indistinguishable from those of large plants of *F. minutulus*. Therefore I consider *F. bambergeri* to be a poorly developed and abnormal form of *F. minutulus*.

REMARK 3: Mueller (1973: 17) remarked "*F. limbatus* is a-typical of the *Fissidentales* the members of which are described as having pitted, longitudinal striations on the outer surface <of the peristome teeth between the trabeculae> (Brotherus, 1924)".

With scanning electron micrographs he showed that in *F. limbatus* the longitudinal striations are composed of papillae.

When seen with a light microscope the intra-trabecular structures of *F. limbatus* are not different from those found in other *Fissidens* species. So possibly those of other species too are composed of papillae.

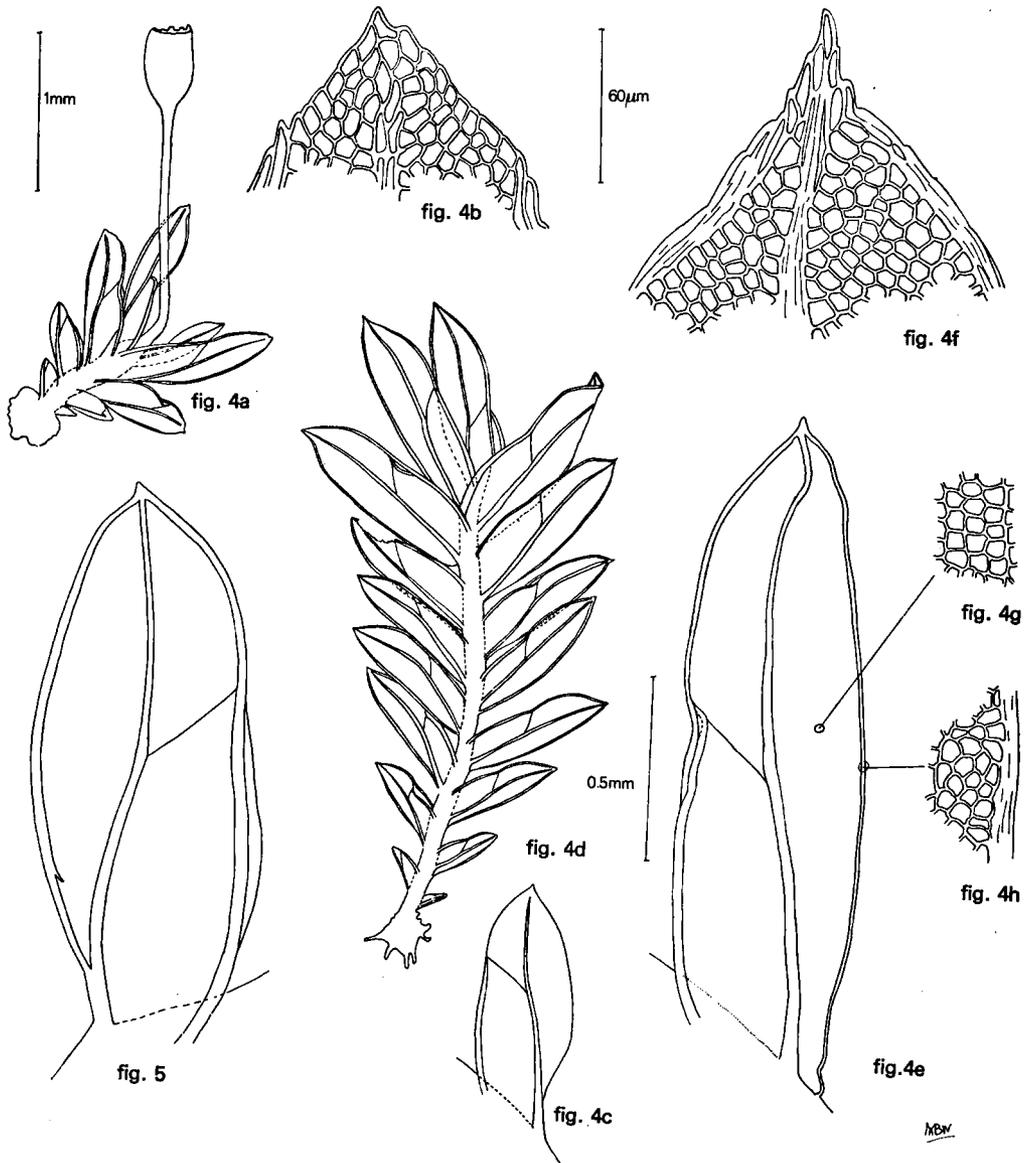


Fig. 4. *F. minutulus* Sull., a: small plant; b: leaf apex of small plant; c: poorly developed leaf; d-h: large plant, d: habit; e: leaf; f: apex; g: cells in the middle of the dorsal lamina and h: border of the middle part of the dorsal lamina. Fig. 4a and b: *Hand* 720, c: type collection of *F. bambergeri* Schimp. ex Milde and d-h: *Macoun* 618. Fig. 5: leaf of *F. ovatifolius* Ruthe (*Richards*, *Tangier*). The same magnification is applied to respectively fig. 4a and d, fig. 4b, f, g and h and to fig. 4c and e and fig. 5.

B. FISSIDENS MINUTULUS SULL., FISSIDENS PUSILLUS (WILS.) MILDE AND FISSIDENS VIRIDULUS (SWARTZ) WAHL

The delimitation of only two of these species, viz. *F. minutulus* Sull. and *F. pusillus* (Wils.) Milde is clear to me. *F. viridulus* (Swartz) Wahl. is not

always easy to recognize as it is very heterogeneous and has, besides, no striking characters.

According to Smith (1970 and 1972) *F. minutulus* Sull. is identical with *F. viridulus* (Swartz) Wahl. However, the type collection of *Dicranum viridulum* Swartz (S, herb. Swartz) does not belong to *F. minutulus* Sull. It is distinct from that species by its larger cells. According to my own observations the cell size in *F. viridulus* is, like it is in most species, rather constant.

Amongst many other samples of *F. pusillus* (Wils.) Milde I have examined an isotype of *F. viridulus* var. *pusillus* Wils. (*Wilson*, Warrington (PC, herb. Bescherelle)). On the ground of all this material I have concluded that:

a. *F. pusillus* (Wils.) Milde is a rather homogeneous species which looks like a miniature *F. crassipes* Wils. ex B.S.G. or *F. rufulus* Bruch et Schimp. in B.S.G. It is characterized by 1) an unbordered acute apex, 2) the terminal position of the antheridia, 3) the rather large cells: (6) 7.5–15 (18) μm long and (4.5) 6–10.5 (12) μm wide and 4) the ecology: it grows on stones in running water or on stones in shady humid places.

b. Contrary to what is generally assumed (Grout, 1936; Jensen, 1939; Norkett, 1962) *F. pusillus* is quite distinct from *F. minutulus* Sull. The most reliable difference between the two is that in cell size: *F. minutulus* has small cells and *F. pusillus* has large ones.

c. According to Smith (1970 and 1972) *F. pusillus* (Wils.) Milde and *F. viridulus* (Swartz) Wahl. are identical. However, the type specimen of *Dicranum viridulum* Swartz does not belong to *F. pusillus*. It is different from that species by the occurrence of axillary antheridial buds (next to which terminal antheridia and antheridia terminal on dwarf male plants are found) and by the acuminate almost completely bordered apex.

C. FISSIDENS SUBIMMARGINATUS PHIL. A NEW SYNONYM OF *F. EXIGUUS* SULL

F. exiguus Sull., 1846. Musci Allegh.: 44. – Type: *Sullivant* Musci Allegh. 182 (FH). – *F. subimmarginatus* Phil., 1884. Rev. Bryol. 11: 56 (do not confuse with *F. submarginatus* Bruch in Kraus, 1846). – *F. exiguus* subsp. *subimmarginatus* (Phil.) Kindb., 1897. Eur. N. Am. Bryin. 2: 171. – Type: *Philibert*, Aix (PC). – *syn. nov.*

The resemblance between these two type collections is striking. The only difference being that *F. subimmarginatus* is slightly better developed: whereas the border of the type of *F. exiguus* never extends beyond the lamina vera and its nerve never reaches the apex, some leaves of the *subimmarginatus* type have traces of a border on the apical and dorsal lamina and in several of the perichaetial leaves the nerve is ex- to per-current.

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