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Fissidens subgen. *Aloma,* the *scariosus*- and *bryoides*-type of peristome in the light of the phylogenetic tree by Suzuki et al.

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The *scariosus* type of peristome and the *bryoides* peristome were considered by Pursell and Bruggeman-Nannenga to be diagnostic for subgen. *Aloma* and subgen. *Fissidens* respectively. Several later authors did not recognize these peristome types nor did they recognize subgen. *Aloma*. In a recent molecular study, however, subgen. *Aloma* emerges as a clade of equal rank to subgenus *Fissidens.* Based on this and on numerous observations of peristomes the *scariosus*- and *bryoides*-type peristome are retrieved from oblivion, compared to each other, re-described and illustrated.

Keywords: *Fissidens*, classification, subgenus *Fissidens*, subgen. *Aloma*, *bryoides*-type peristome, *scariosus*-type peristome

Brotherus (1901, 1924) and Fleischer (1904) used peristome characters for the classification of *Fissidens*. They distinguished between taxa with nodose and taxa with spirally ornamented filaments.

Allen (1980) published a SEM-study of peristome-types in *Fissidens* and concluded that in some cases these are correlated with gametophytic groups. He described the *scariosus*- and *bryoides*-types of peristome using characters of both the exterior and the interior layer of the peristome.

Bruggeman-Nannenga and Berendsen (1990) amended Allen's *scariosus*- and *bryoides*-types of peristome based partly on SEM and partly on light microscope observations. Their types are based on features of the exterior peristome layer, recognizing five main types of peristome each with a strong correlation to a gametophytic group.

Ishihara and Iwatsuki (1992) studied different features of peristomes in *Fissidens* and discerned two types of peristome: one not making hygroscopic movements and having nodose filaments, the other making hygroscopic movements and having spirally thickened filaments. The first is found in subgenus *Serridium* and *Pachyfissidens* while the second is found in all other infrageneric taxa.

Pursell and Bruggeman-Nannenga (2004) published 'refinements to the infrageneric classification of the Fissidentaceae' most amendments being based on the number of exothecial cells around the capsule circumference, peristome- and the costal types. The existence of transitional forms led to a reduction of several of Brotherus' sections into *Fissidens* subg. *Aloma* (Kindb.) Pursell & Brugg.-Nann. (in the following referred to as subgen. *Aloma* P&BN). Accordingly, this subgenus is sporophytically homogeneous but gametophytically rather heterogeneous. This classification was followed by Beever (2014).

Suzuki and Iwatsuki (2007) published 'new refinements of the infrageneric classification'. They reduced the *bryoides*- and *scariosus*-peristome types into one, the *fissidens*-type. Consequently, they did not recognize subgen. *Aloma* P&BN which is based mainly on the *scariosus* type peristome and the presence of only 32 exothecial cells around the capsule.

Suzuki et al. (2018) published a molecular study in which subgen. *Aloma* P&BN is resolved as a clade 'subgen. *Fissidens* sect. *Polyodiopsis* + sect. *Areofissidens* + sect. *Aloma* + sect. *Semilimbidium*'. In other words, in addition to sporophytic evidence there is now also molecular support for subgen. *Aloma* P&BN. This insight makes it necessary to reconsider the peristome types that have been subsumed into the *fissidens*-type of peristome.

Material and methods

A study of peristomes is complicated for more than one reason. Many collections lack sporophytes. When present the peristomes are frequently damaged. Some peristomes are thin, transparent and poor in contrast. Moreover, many peristomes are hygroscopic and strongly incurved at the bifurcation when wet, making observations of this area difficult. Peristomes are best studied when the operculum has been freshly detached before they become incurved.

For a study of the peristome-types it is not only necessary to understand the general structure of peristomes, it is also prerequisite to understand the peristome types and to know what one is looking for. Therefore, the *scariosus*- and *bryoides*-type are here elaborately described and illustrated. Oil-immersion and a lot of focusing are necessary assets in distinguishing the types.

General structure of peristomes

Peristomes are complicated structures and often hard to analyze with the light-microscope. Basic to the study of peristomes is a good understanding of their structure.

Fissidentaceae have haplolepidous peristomes i.e. the peristomes are composed of a single row of 16 teeth.

Each tooth has a basal undivided part. At the bifurcation it is split into two filaments.

Each tooth is composed of two layers of cells (Plate 1: 1, 1: 4), an exterior (OPL) and an interior layer (IPL). During the formation of the tooth, the walls of the OPL- and IPL-cells become partly thickened and partly disappear, the cells become 'roofless'.

Each tooth is built up by a single column of OPL cells (Plate 2: 4) and two columns of half IPL-cells (the other half-cell is part of the adjoining tooth). The borderline between these half cells is a characteristic zigzag-line (Plate 2: 5).

The most important features of a tooth are the horizontal walls, the trabeculae and the 'floor' between, called the lamella. Successive trabeculae are sometimes connected by vertical walls. In the *bryoides*-type the trabeculae of the undivided part are distinct and protruding (Plate 2: 3). In the *scariosus*-type of peristome the trabeculae (Plate 1: 5–6) do not or hardly protrude and often have an incrassate margin.

All descriptions in this paper are based on light microscopic observations of the OPL of the undivided part and bifurcation.

Results and discussion

Subgenus *Aloma* P&BN is composed of several not sharply distinct gametophytic groups, sections and subgenera in Brotherus (1924). Because of the occurrence of transitional species Pursell and Bruggeman-Nannenga (2004) united

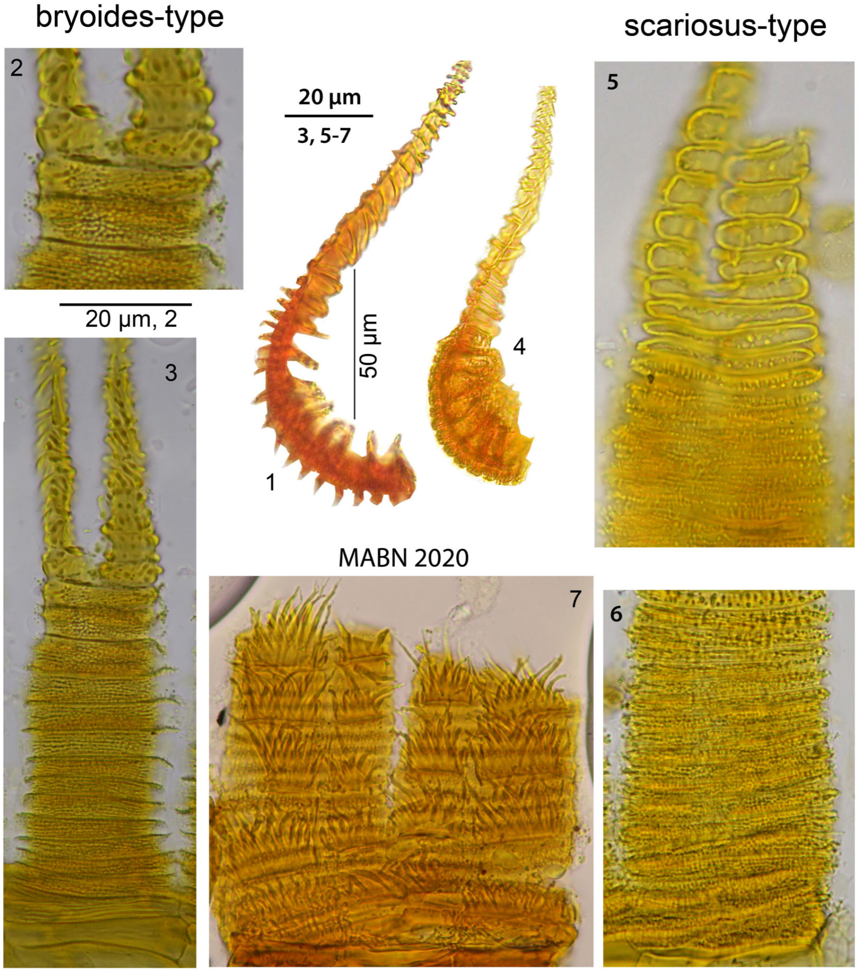

Plate 1. Comparison of *bryoides*- and *scariosus*-type peristomes. (1–3) *bryoides*-type; (1) tooth in side-view showing protruding trabeculae (filament on the right), (2) bifurcation, (3) exterior side of tooth with high protruding trabeculae (4–8) *scariosus*-type; (4) side view of tooth, filament on the right; (5) exterior side of tooth showing continuous walls surrounding the OPL-cells at the bifurcation; (6) undivided part from same tooth as (5), but focused slightly differently, (7) fimbriate IPL trabeculae. (1) From *F. megalotis* subsp. *helictocaulos* (Pócs 8678/R), (2) and (3) from *F. becketii* (Polhill & Paulo B9), (4) from *F. zollingeri* (D. Vital 7657), (5–6) from *F. zollingeri* (Van Zanten 116A) and (7) from *F. usambaricus* (Hylander 4527).

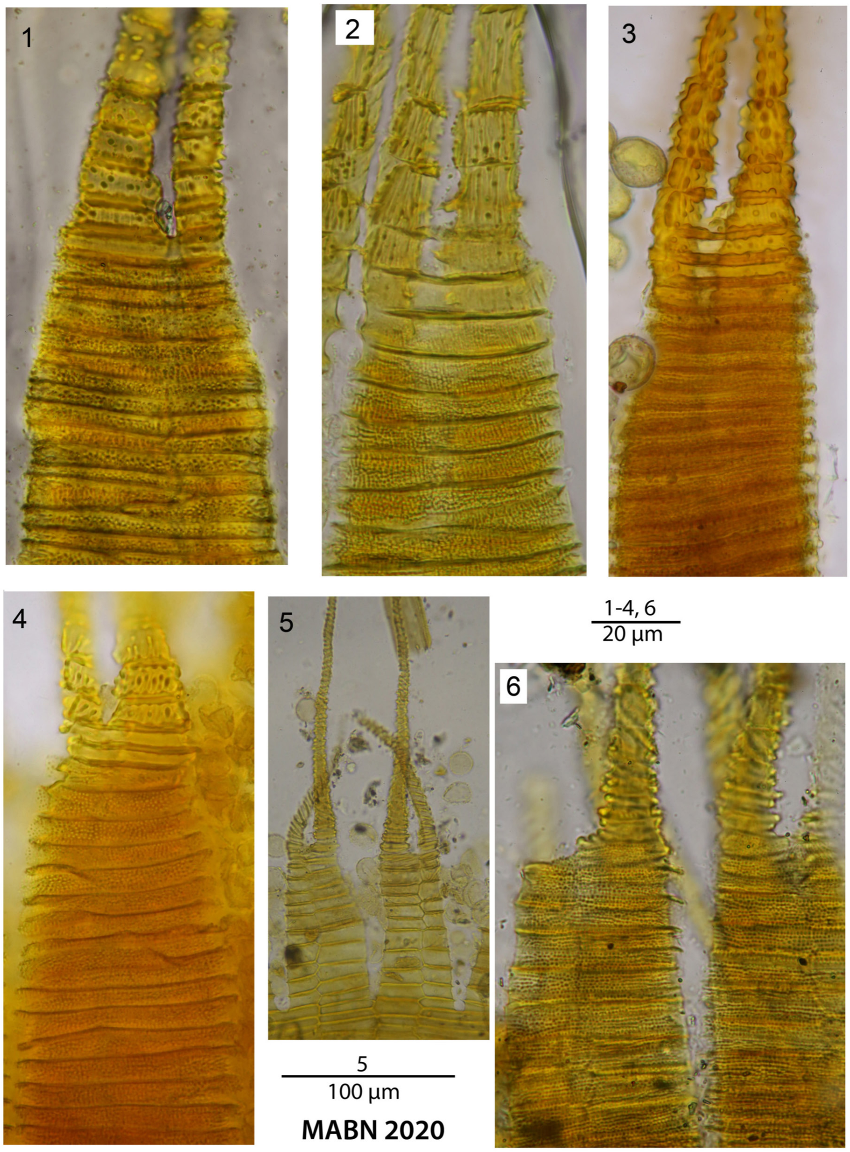

Plate 2. *Bryoides*-type peristomes (see also Plate 1: 1–3). (1) *F. rufulus*, (2) *F. rigidulus*, (3) *F. bryoides* var. *bryoides*, (4) *F. gladiolus*, (5–6) *F. curvatus*, (5) interior side peristome, (6) exterior side peristome. (1) From Bruggeman-Nannenga 403 (L), (2) from Berggren 29, (3) from Bruggeman-Nannenga 1292, (4) from Jones 572, (5–6) from Herzog 2984.

these taxa into subgen. *Aloma* P& BN. Sporophytically, this subgenus is well defined by two characters, viz. ± 32 exothecial cells around the capsule circumference and a unique peristome-type, the *scariosus*-peristome.

Suzuki and Iwatsuki (2007) reduced the *scariosus*- and *bryoides*-peristome types into one, the *fissidens*-type peristome. In doing so they undermined the morphological basis for subgen. *Aloma* P&BN. Consequently, they did not recognize this subgenus.

However, in a molecular study (Suzuki et al. 2018) subgen. *Aloma* P& BN re-appears as a clade ('subgen. *Fissidens* sect. *Polyodiopsis* + sect. *Areofissidens* + sect. *Aloma* + sect. *Semilimbidium*') and the sections and subgenera united by Pursell and Bruggeman-Nannenga (2004) appear as subclades, resulting in the need for their reinstatement.

Numerous observations made by me since the 1990-SEM study (Bruggeman-Nannenga and Berendsen 1990) also confirm the *bryoides*- and *scariosus*-type of peristomes to be clearly distinct and characteristic for subgen. *Fissidens* and *Aloma* respectively, and that ± 32 exothecial cells around the capsule is characteristic of subgen. *Aloma*. Only a few exceptions were seen. For instance, the subgen. *Aloma*-species *F. exilis* Hedw., *F. dealbatus* Hook. f. & Wilson, *F. flabellulus* Thwaites & Mitt. var. *flabellulus* and *F. afropapillosus* P. de la Varde all have more than 40 files of exothecial cells. Furthermore, quite a few, particularly corticolous and aquatic species, have anomalous peristomes, suggesting that these are adaptations to the environment. Corticolous species with anomalous peristomes are, for instance, *F. gardneri* Mitt., *F. punctulatus* Sande Lac. and *F. lagenarius* Mitt. Examples of aquatic species with anomalous peristomes are *F. fontanus, F. berteroi* (Mont.) Müll. Hal. and *F. acacioides* Schrad. var. *acacioides*).

The above makes it clear the *scariosus*- and *bryoides*-type of peristome are valuable characters to distinguish subgen. *Fissidens* from subgen. *Aloma* P&BN. It has thus become imperative to retrieve these peristome-types from oblivion.

Teeth of both types are hygroscopic and have ‘spirally’ ornamented filaments.

Bryoides-type peristome (Plate 1: 1–2)

Undivided basal – OPL part with conspicuous, high, thin, trabeculae protruding well above the low lamellar ornamentation.
Bifurcation – OPL is rather variable.
Distal filaments spirally ornamented (Plate 2: 5).

scariosus-type of peristome (Plate 1: 6)

Undivided part – OPL (Plate 1: 4–6). The trabeculae do not or hardly protrude above the lamellar ornamentation. If in doubt, side-viewing the tooth will be helpful. The lamellae often show rows of coarse ‘papillae’ (Plate 3: 3, 3: 5). In many species the OPL trabeculae of the undivided part have a thickened margin.
The bifurcation – OPL. Towards the bifurcation the lamellar ornamentation becomes less conspicuous and the walls surrounding the OPL cells become distinct (Plate 1: 5), encircling the cell completely. Beyond the splitting of the tooth the OPL cells are torn into two halves each surrounded by a wall on three sides.
Distal filaments spirally ornamented.
The IPL trabeculae of the undivided part of the *scariosus* type frequently have fimbriae (Plate 1: 7; Allen 1980: Fig. 9, 10).

Plate 1 shows distinctions between the two types. The *bryoides*-type differs from the *scariosus*-type by the high protruding OPL-trabeculae of the undivided part (Plate 1: 3). In the *scariosus*-type these trabeculae do not, or hardly, protrude (Plate 1: 6). Furthermore, the two types differ in the bifurcation: in the *scariosus*-type the OPL-cells are completely surrounded by walls (Plate 1: 5).

Plate 2 shows examples of *bryoides*-type peristomes. With the exception of Plate 1: 4 and 1: 7 the figures are from species with typical subgen. *Fissidens* gametophytes, viz. limbate on all laminae and small to medium sized, smooth laminal cells. *Fissidens gladiolus* (Plate 2: 4) is a species that combines an unmistakable *bryoides*-type peristome and more than 40

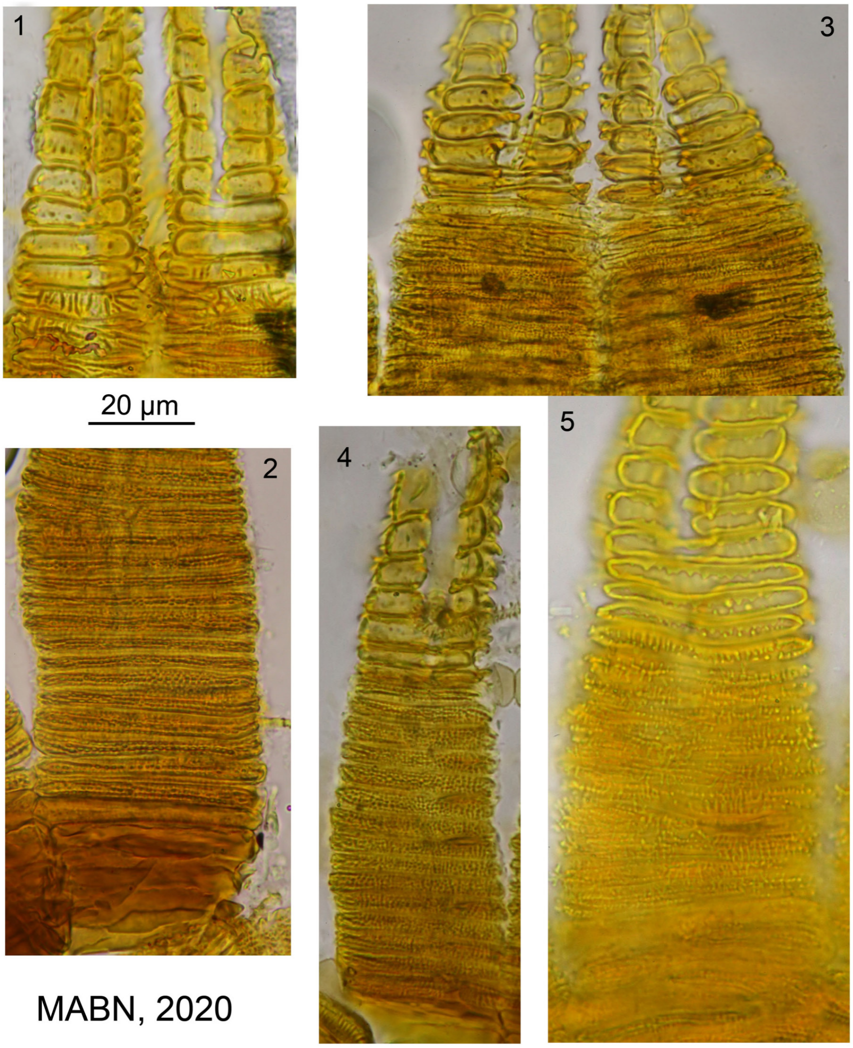

Plate 3. *Scariosus*-type (1). (1–2) *F. usambaricus* (ecostate), (1) bifurcation, (2) undivided part, (3) *F. flaccidus* (limbate, very large cells), (4) *F. bogoriensis* (very large cells, variably limbate), (5) *F. zollingeri* (limbate, vaginant laminal cells large and inflated). (1) From Chandler 1852, (2) from Hylander 4527, (3) from D. Vital 5036, (4) from *F. bogoriensis* shrine of Hirauchi, Iwatsuki et al. s.n. and (5) from Van Zanten 116A.

files of exothecial cells with a reduced gametophyte. *Nanobryum dummeri* Dixon, the type species of *Nanobryum*, is a synonym of *F. gladiolus*. It is considered to belong in subgen. *Fissidens* (Pursell and Bruggeman-Nannenga 2004).

Plate 3–5. Examples of *scariosus*-type peristomes arranged by gametophytic group.

Plate 3. Ecostate species (*Polypodiopsis*), species with large cells (*Areofissidens*) and *F. zollingeri* Mont. Gametophytically this species could be placed in subgenus *Fissidens.* However, the sporophyte having ± 32 exothecial cells around the capsule and a *scariosus*-type peristome, clearly indicates subg. *Aloma* P&BN. Moreover, the very large and often inflated cells of the vaginant laminae suggest sect. Areofissidens. This species has not been sequenced.

Plate 4. Species with smooth laminal cells. Traditionally, species with smooth cells and (±) elimbate leaves are classified in sect. *Aloma* (Brotherus 1924, Suzuki and Iwatsuki 2007).

However, in the phylogenetic tree by Suzuki et al. (2018) some of these species are in clade : sect. *Aloma* (*F. exilis*, *F. pseudoclosteri* and *F. takayukii*), whereas *F. pellucidus* is in clade sect. *Semilimbidium*. Here the *scariosus* type peristome of both *F. exilis* and *F. pellucidus* are illustrated. It will be interesting to see what further molecular studies will teach us about elimbate species. From a nomenclatorial point of view it is important to study the DNA of *F. pauperculus*, the type species of *Aloma*.

Plate 5. Species with pluripapillose or mammillose cells, limbidia variable (Semilimbidium).

Further contemplations

Subgenus *Aloma* P&BN is gametophytically heterogeneous and it is hard, if not impossible, to find gametophytic features shared by all species. Several authors Brotherus (1901, 1924), Suzuki and Iwatsuki (2007) and Suzuki et al. (2018) recognized several sections and subgenera in subgen. *Aloma* P&BN (Table 1).

It is interesting to note that in the phylogenetic tree by Suzuki et al. (2018) subgen. *Aloma* P&BN is a clade of equal rank to subgenus *Fissidens* subgen. *Fissidens* and that several subclades are resolved that represent some of Brotherus' and

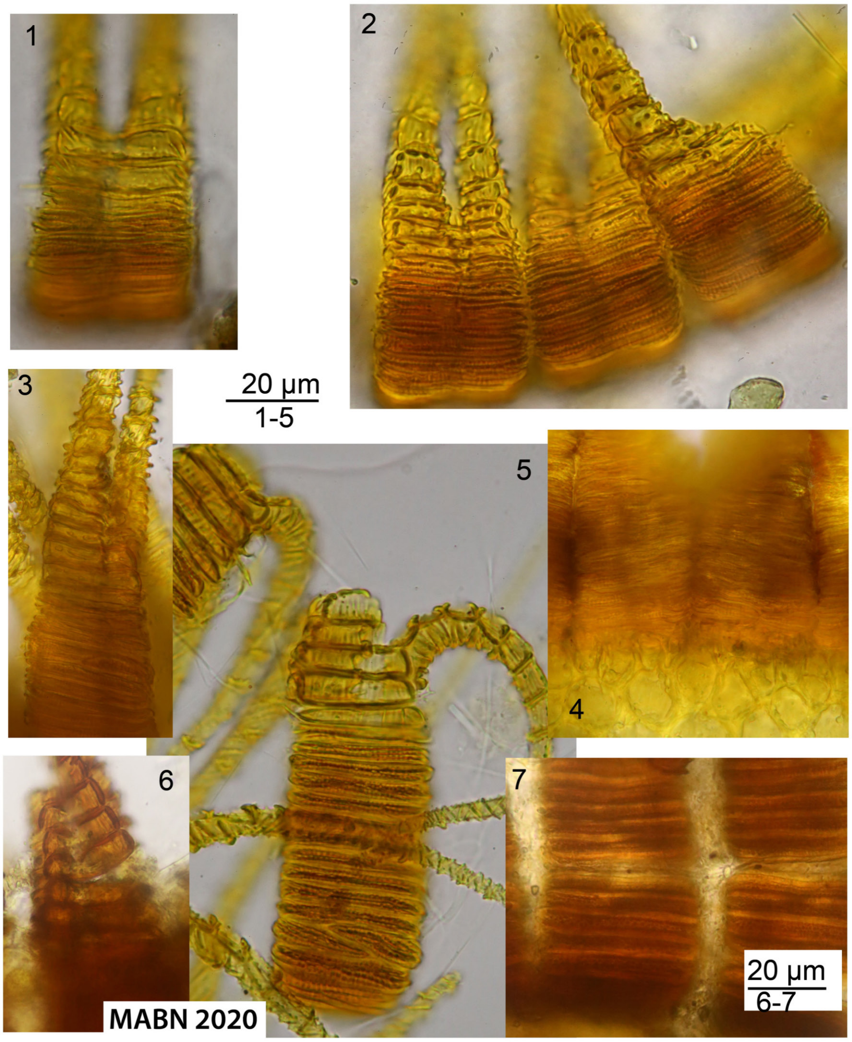

Plate 4. *Scariosus*-type (2) species with smooth cells and ± elimbate to semilimbate leaves. (1–2) *F. exilis*, (3–4) *F. flabellulus*, (5) *F. pellucidus*, (6–7) *F. porrectus*. (1–2) from Sollman & H. Waltje s.n., (4) from C.M 142 (isotype), (5) from Vital, Griffin and Yano 4273, (6–7) from Lisowski 223.

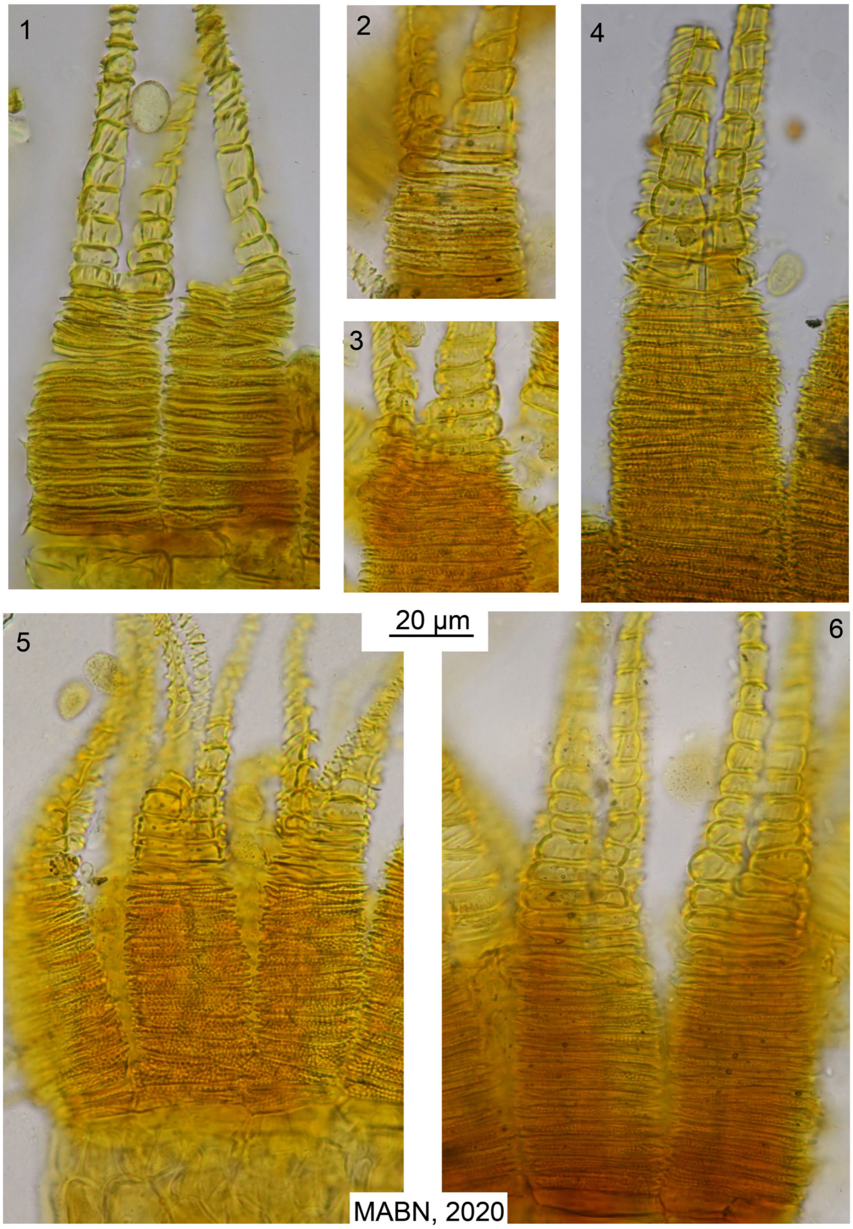

Plate 5. *Scariosus*-type peristomes (3), species with pluripapillose or mammillose cells. (1) *F. pallidinervis* (pluripapillose, ± elimbate), (2) *F. submarginatus* (sharply mammillose, semilimbate), (3) *F. wichurae* (pluripapillose, limbidia on basal part of the vaginant laminae of most leaves, (4) *F. dasyphus* (pluripapillose, limbate on all laminae), (7) *F. serratus* (mammillose, elimbate), (8) *F. thwaitesii* (mammillose, semilimbate). (1) from Richards 6978, (2) from Krauss s.n., (3) from Meijer B 5780, (4) from Kovács 18A, (5) from Crosby 7861 and (6) from Bunnak 258.

Suzuki and Iwatsuki's taxa (Table 1). It is clear that when more molecular data from more species becomes available the infrageneric classification of the Fissidentaceae will have to be reconsidered. This will almost certainly lead to new combinations. This, however, is outside the scope of this publication and in my opinion should only be done when significantly more molecular results become available.

List of illustrated specimens

Fissidens androgynus Tanzania, Nguru Mts in Morogoro District. Below Kwasenjuga summit S of Maskati, Kis & Pócs 9112/AM (EGR, L); *F. becketii* Mitt. Tanzania, Dodoma Distr., Chenene Hills, Polhill & Paulo B9 (PC, E); *F. bogoriensis* M. Fleisch., Japan. Kyushu, Kagoshima-ken, Isl. Yakushima, shrine of Hirauchi, 26 X 1975, Iwatsuki et al. s.n. (L); *F. bryoides* Hedw., the Netherlands, Zuid Limburg, Geuldal, Bruggeman-Nannenga 1292 (L); *F. curvatus* Hornsch., as *F. bockii* Herzog, Bolivia, in der Bachschlucht Tarujumaña, 3300 m, Herzog 2984 (PC isotype); *F. dasyphus* Ghana, Afrantwo, 26 km NW of Kumasi, Kovács 18A (PC); *F. exilis* Hedw., the Netherlands, Friesland, Barthehiem, essenaanplant op klei, terr.. IVON 6.32.31. 18 II 2009, P. Sollman & H. Waltje s.n. (private herb. P. Sollman);

Table 1. Some historic interpretations of infrageneric taxa of *Fissidens*. Subgen. *Aloma* P&BN corresponds with the clade 'subgen. *Fissidens* sect. Polyodiopsis + sect. Areofissidens + sect. *Aloma* + sect. Semilimbidium'.

Brotherus 1924	Suzuki and Iwatsuki 2007	Pursell and Bruggeman-Nannenga 2004	Suzuki et al. 2018
Subgen. *Polypodiopsi*s	Subgen. *Aneuron*	Subgen. *Aloma*	Subclade *Polyodiopsis* in clade 'subgen. *Fissidens* sect. *Polyodiopsis* + sect. *Areofissidens* + sect. *Aloma* + sect. *Semilimbidium'**
Subgen. *Fissidens* sect. *Weberiopsis*	Subgen. *Fissiden*s sect. *Fissidens*	Subgen. *Aloma*	Subclade Areofissidens in clade 'subgen. *Fissidens* sect. *Polyodiopsis* + sect. *Areofissidens* + sect. *Aloma* + sect. *Semilimbidium'**
Subgen. *Fissidens* sect. *Reticularia*	Subgen. *Fissidens* sect. *Fissidens*	Subgen. *Aloma*	Subclade *Areofissidens* in clade 'subgen. *Fissidens* sect. *Polyodiopsis* + sect. *Areofissidens* + sect. *Aloma* + sect. *Semilimbidium'**
Subgen. *Fissidens* sect. *Semilimbidium*	Subgen, *Fissidens* sect. *Semilimbidium*	Subgen. *Alom*a	Subclade *Semilimbidium* in clade 'subgen. *Fissidens* sect. *Polyodiopsis* + sect. *Areofissidens* + sect. *Aloma* + sect. *Semilimbidium'**
Subgen. *Fissidens* sect. *Aloma*	Subgen. *Fissidens* sect. *Aloma*	Subgen. *Aloma*	Partly in subclade *Semilimbidium* in clade 'subgen. *Fissidens* sect. *Polyodiopsis* + sect. *Areofissidens* + sect. *Aloma* + sect. *Semilimbidium'** AND Partly in subclade *Aloma* in clade 'subgen. *Fissidens* sect. *Polyodiopsis* + sect. *Areofissidens* + sect. *Aloma* + sect. *Semilimbidium'**
Subgen. *Fissidens* sect. *Pycnothallia*	Subgen. *Fissidens* sect. *Fissidens*	Subgen. *Aloma*	Not included
Subgen. *Fissidens* sect. *Crenularia*	Subgen. *Fissidens* sect. *Semilimbidium*	Subgen. *Aloma*	Not included
Subgen. *Fissidens* sect. *Bryoidium*	Subgen. *Fissidens* sect. *Fissidens*	Subgen. *Fissidens*	Clade Subgen. *Fissidens* sect. *Fissidens*
Subgen. *Fissidens* sect. *Heterocaulon*	Subgen. *Fissidens* sect. *Fissidens*	Subgen. *Fissiden*s	Clade Subgen. *Fissidens* sect. *Fissidens*
Subgen. *Fissidens* sect. *Pachylomidium*	Subgen. *Fissidens* sect. *Fissidens*	Subgen. *Fissidens*	Clade Subgen. *Fissidens* sect. *Fissidens*
Subgen. *Octodiceras*	Subgen. *Octodiceras*	Subgenus *Octodiceras*	Subclade in clade Subgen. *Fissidens* sect. *Fissidens*

Fissidens flabellulus Thwaites & Mitt. var. *flabellulus*, Ceylon (Sri Lanka), Central province, C.M 142 (isotype: H-BR); *F. flaccidus* Mitt., Brazil, Minas Gerais State, ca 20 km E-NE of Iturama, D. Vital 5036 (L); *F. gladiolus* Mitt.-Uganda, Budongo Forest, Bunyore province, Jones 572 (PC); *F. megalotis* subsp. *helictocaulos* (Müll. Hal.) Brugg.-Nann., Tanzania, Meru Mts valley of Engare Olmotonyi behind Forest Training Institute, Pócs 8678/R (EGR); *F. pallidinervis* Mitt., Ghana, Atewa Range Forest Reserve near Asiakwa Camp, 6°12′N, 0°03′W, Richards 6978 (MO, L); *F. pellucidus* Hornsch., Brazil, Amazonas State, Reserva Campina, along road Manaus-Caracarai, 60 km, Manaus; on rotten trunk, in humid forest. I VIII 1074. D Vital, Griffin and Yano 4273 (SP); *F. porrectus* Mitt., GUINEA, Fouta-Djallon, près de Dalaba, Lisowski 223 (KRAM-C); *F. rigidulus* Hook. f. & Wilson – New Zealand, insula australis, Bealy. Berggren 29, 1874 (NY); *F. rufulus* Schimp. in Bruch, Schimp. & W. Gümbel. France, dept. Hautes Pyrenées, 3.5 km N de Ferrières, ± 500 m, Bruggeman-Nannenga 403 (L); *F. serratus* Müll. Hal., var. *serratus*. South Africa. Natal Cathkin Peak Forest Reserve, ca 53 km E of Estcourt,1500 m, Crosby 7861 (L); *F. submarginatus* Bruch in Krauss. South Africa, Natal, in silvis prope Umlusir, Krauss s.n. (PC); *F. thwaitesii* Paris – Thailand, S.E. Chanburi, Makhma, Khao Mai Kaew, Bunnak 258 (L); *F. usambaricus* Broth. – Ethiopia, Kaffa. Bonga, 1.5 km SE of central Bonga, Hylander 4527 (S, L); Uganda, Miles and Masaka Road. Forest, Chandler 1852 pp (BM 2556M-80); *F. wichurae* Broth. & M. Fleisch. West Java, Gegerbintang-ridge nr Tjibodjas, 1500–1700 m, W. Meijer B 5780 (L); *F. zollingeri* Mont. – Nieuw Guinea, Sterrengebergte, Tanah-Merah, 50 m; Van Zanten 116A (L); Brazil, Minas Gerais State, Município de Passos. 20°43′S, 46°47′W, D. Vital 7657.

The following species were also included in the DNA study by SIT, 2018 *F. becketii, F. bogoriensis, F. bryoides* subsp. *bryoides, F. exilis, F. flaccidus, F. pellucidus* and *F. pallidinervis*.

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