

On the anatomy of the costa in *Fissidens*

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Abstract. Based on a study of ca. 120 *Fissidens* species covering all sections and subgenera, three types of costae are recognized. One type is characteristic of sect. *Amblyothallia* and of *F. asplenioides*, *F. fasciculatus* and *F. plumosus* (the fasciculatus-group); the second of subg. *Serridium*, subg. *Fissidens* sect. *Crispidium* and *F. grandifrons* (subg. *Pachyfissidens*) and the third type of subg. *Fissidens* sect. *Fissidens*, sect. *Aloma*, sect. *Crenularia*, sect. *Semilimbidium*, sect. *Pycnothallia*, and sect. *Areofissidens*, subg. *Octodiceras*, and subg. *Sarawakia*.

Introduction

In a previous paper (Bruggeman-Nannenga & Berendsen 1988) it was shown that the peristome in the Fissidentaceae furnishes good additional characters to those traditionally used in the classification of the family into subgenera and sections. Unfortunately, many specimens of *Fissidens* are sterile and some species are known only in the sterile condition. Moreover, there are many species with anomalous peristomes. The structure of the costa appears to be another useful character in the classification of the family.

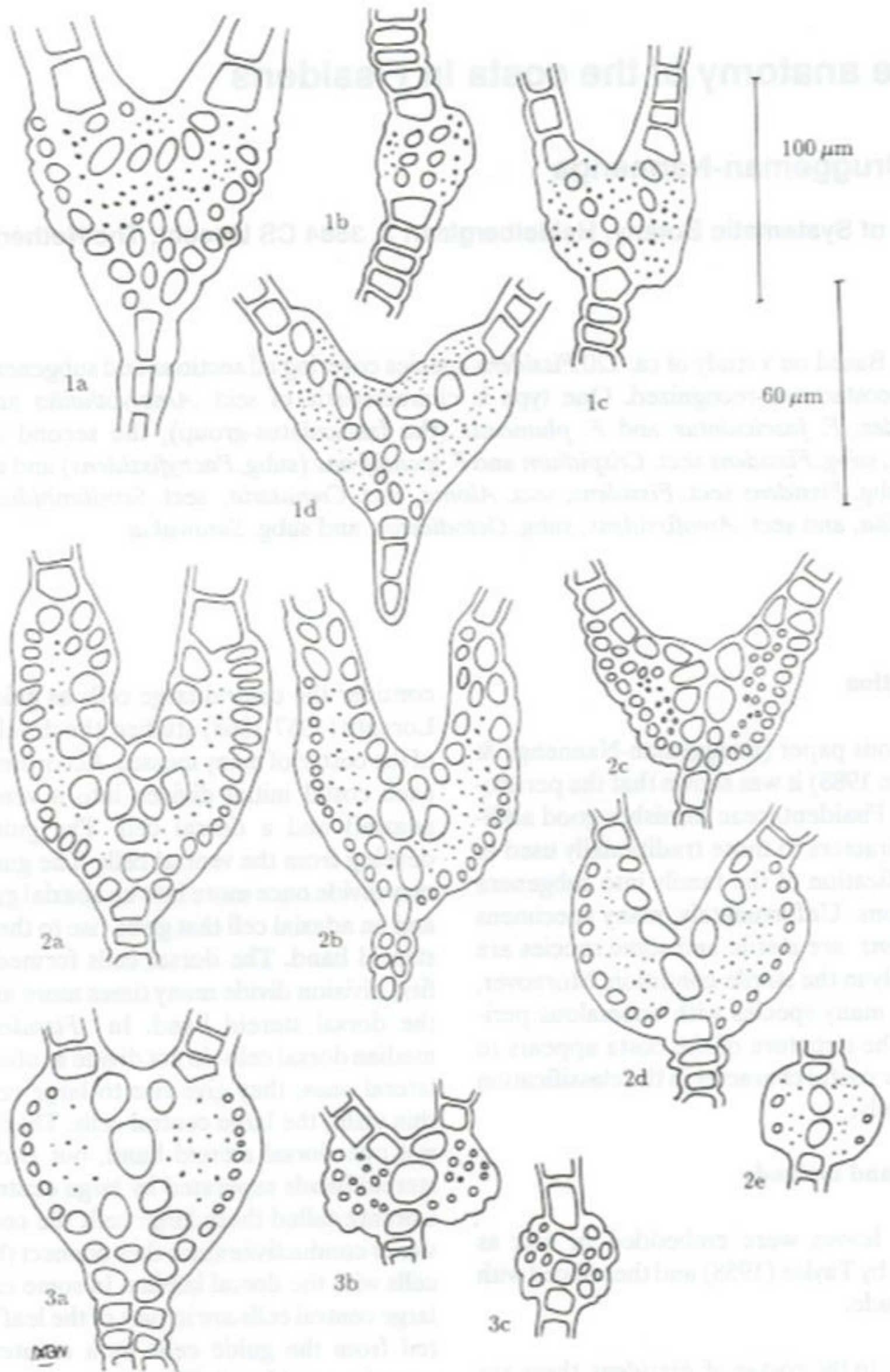
Material and methods

Stems or leaves were embedded in wax as described by Taylor (1958) and then sliced with a razor blade.

Cell types. In the costae of *Fissidens* there are three types of cells: guide cells, large central cells, and small cells that vary from stereids to substereids to cells with somewhat larger lumina, and slightly incrassate walls. Most authors

consider the central large cells as guide cells. Lorentz (1867-1868) studied the development of the costae of many mosses. According to him each costal initial divides into a ventral (= adaxial) and a dorsal cell. The guide cells develop from the ventral cells. The guide cells may divide once more into an abaxial guide cell and an adaxial cell that gives rise to the ventral stereid band. The dorsal cells formed by the first division divide many times more and form the dorsal stereid band. In *Fissidens* the median dorsal cells do not divide as often as the lateral ones; they give rise to large cells with thin walls, the large central cells. Thus there is not one dorsal stereid band, but two lateral stereid bands separated by large central cells. Lorentz called these large cells the conjunctivae or conductivae since they connect the guide cells with the dorsal lamina. In some cases the large central cells are in part of the leaf separated from the guide cells by a uninterrupted dorsal stereid band (Fig. 1a).

The following descriptions of the costal types apply to the duplicate part of the leaf since the



The following descriptions of the stem types apply to the duplicate part of the leaf base...

Cell types in the cortex of *Festuca* stems are three types of cells: guide cells, large cortical cells, and small cells that vary from strands to subside to cells with somewhat larger walls. Most subepi- and slightly increased walls. Most subepi-

Table 1: The distribution of peristome types, number of exothecial cells and costa types in the Fissidentaceae (adapted from Bruggeman-Nannenga and Berendsen, 1988).

taxon	peristome	exothecial cells	costa

Group Ia			
Octodiceras	?	b	III
Sarawakia	B, ?	b	III
Fissidens	B	b	III
Nanobryum	B	b	III, ?

Group Ib			
Aneurion	S	a	-
Areofissidens	S	a	III
Aloma	S	a	III
Crenularia	S	a	III
Semilimbium	S	a	III
Pycnothallia	S	a	III

Group II			
Crispidium	Z	b	II
Serridium	T (N)	b	II
F. grandifrons	T	b	II

Group III			
Amblyothallia	Si	b	I
"group fasciculatus"	F	b	I-

Peristome: ? = not belonging to one of the main types and/or reduced, B = bryoides-type, F = fasciculatus-type, N = nobilis-type, S = scariosus-type, Si = similiretis-type, T = taxifolius-type, Z = zippelianus-type. Exothecial cells: a = circa 32 and not more than 40 on the capsule periphery, b = more than 40. Costa: I = oblongifolius-type, II = taxifolius-type and III = bryoides-type, ? = reduced, - = absent.

NB. The fasciculatus-group consists of *F. asplenioides*, *F. fasciculatus* and *F. plumosus*.

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Fig. 1: Oblongifolius-type. 1a: *F. maschalanthus* Mont., Chili, Crosby 12.041 (PAC), 1b and d: *F. fasciculatus* Hornsch., South Africa, Esterhuysen 25464 (L) and 1c: *F. oblongifolius* Hook. f. & Wils., Society Isl., De Sloover 20992 (U).

Fig. 2: Showing some of the variations found in the taxifolius-type. 2a: *F. areolatus* Griff., Bhutan, Long 10577 (E), 2b: *F. dubius* P. Beauv., the Netherlands, Nannenga-Bremekamp 6 (hb. Bruggeman-Nannenga), 2c: *F. taxifolius* Hedw., France, Le Sauget, Bruggeman-Nannenga s.n. (hb. Bruggeman-Nannenga), 2d and 2e: *F. zippelianus* Doz. & Molkenb., Bhutan, Long 7746 (E).

Fig. 3: Bryoides-type. 3a: *F. rigidulus* Hook. f. & Wils., New Zealand, Wharerata, Sainsbury s.n. (BM), 3b: *F. flexinervus* Mitt. Surinam, Florschütz 2057 (U) and 3c: *F. diversifolius* Broth., India, Waistakhen, Sedgwick s.n. (L).

The left scale bar applies to fig. 2a - c and 3b; the right one applies to all other figures.

structure of the costa in the simple, upper part was not systematically studied. The structure of the costa at the base, middle and upper part of the vaginant laminae may not be the same. There may also be differences between the costae of vegetative and perichaetial leaves. Observations cited in this paper, unless otherwise stated, are from the middle part of the vaginant laminae of vegetative leaves.

Important characters appear to be: 1) The number of guide cells, 2) the number of bands of small cells, 3) whether the epidermis cells are differentiated (i.e. have larger lumina than the inner cells) and 4) whether the vaginant laminae at their juncture with the costa are formed by stereids or substereids and guide cells (Fig. 1d, 2a-d) or by laminal cells (Fig. 3a and b).

As a rule only one collection per species is cited in the examined material. Institutional (abbreviated) and personal herbaria are cited in brackets.

Description of the types of costae

I. *Oblongifolius*-type (Fig. 1a - d). This is the most distinct of the three types. It is characterized by:

1) 4 - 7 (-16) guide cells which form a U or V.
2) The 1 - 5 large central cells are usually arranged in 2 (-3) rows (Fig. 1c).

3) Two lateral and one adaxial band of substereids or stereids. In *F. fasciculatus* and *F. plumosus* these bands are larger in the basal part of the leaf (Fig. 1d), more distally they become smaller. In *F. asplenoides* the adaxial band may be stereid or substereid not introduced earlier. In *F. maschalanthus*, *F. asplenoides* and *F. fasciculatus* the dorsal stereid band (see material and methods) is not always divided into two lateral bands in the basal part of the vaginant laminae (Fig. 1a).

4) Epidermal cells are undifferentiated (Fig. 1c-d), except in *F. asplenoides* and *F. mascha-*

lanthus (Fig. 1a).

5) The vaginant laminae, at their juncture with the costa, are composed of laminal cells (Fig. 1a, c). In the basal part of the leaves of *F. plumosus* and *F. fasciculatus* these areas of the vaginant laminae are composed of stereids and guide cells (Fig. 1d).

In the costa of the simple, upper part of the leaf the large cells are often arranged into 2 rows (Fig. 1b). This arrangement may be characteristic of this type, but is not found in *F. asplenoides* and *F. pallidus*, in which there is a single row. In *F. maschalanthus* there is a row that is double in places. In *F. plumosus* the arrangement varies from a cluster of cells that is wider in the lateral direction than in the dorso-ventral direction to just a single row near the apex of the leaf.

Examined species: *F. allenianus* Brugg.-Nann. & Pursell, Mexico, Mac-Farland & Sharp 9195 (PAC); *F. asplenoides* Hedw., Malawi, Long 12567 (E, Bruggeman-Nannenga) and USA, Louisiana, Reese 10678 (U); *F. delicatulus* Aongstr., Hawaii, Hoe 23030 (U); *F. dendrophilus* Brugg.-Nann. & Pursell, Brazil, Sehnem 300 (FH-Bartr. type); *F. fasciculatus* Hornsch., South Africa, Esterhuysen 25404 (L); *F. imbricatus* Britt. & Bartr., Cuba, La Muleta, Borhidi & Duarte (PC); *F. maschalanthus* Mont., Chili, Crosby 12.041 (PAC); *F. microcarpus* Mitt., Banks of Nunn, Mann s.n. (BM); *F. oblongifolius* Hook. f. & Wils., Society Isl., De Sloover 20992 (U); *F. pallidus* Hook. f. & Wils., Australia, New South Wales, Streimann 051025 (L); *F. plumosus* Hornsch., South Africa, Arnell 1968 (PC); *F. pseudostipitatus* C. Muell., Brazil, Yano 445 (SP, Bruggeman-Nannenga); *F. radicans* Mont., Surinam, Lanjouw & Lindeman 2288 (U) and French Guyana, Aptroot 15246 (U); *F. schusterii* Iwats. & Wu, China, Boxi, Chen (HIRO); *F. similiretis* Sull., Cuba, Schubert Mi54 (PC-Bizot).

The next two types of costae differ from the first type by lacking an adaxial band of stereid cells.

II. *Taxifolius*-type (Fig. 2a - e). This type is characterized by:

1) (2-) 4 - 12 peripheral guide cells.

2) 1 - 8 large, central cells, which are usually

arranged in a single dorso-ventral row (Fig. 2d), but occasionally into two rows (Fig. 2c) or are an irregular mass (Fig. 2a).

3) Two lateral stereid or substereid bands.

4) Epidermal cells which have relatively wide lumina, except in *F. glaucescens* and *F. subangustus*.

5) The juncture of the vaginant laminae and costa is composed of stereids or substereids and guide cells.

As far as has been determined, the costa in the simple, upper part of the leaf has a single row of large cells (Fig. 2e), except in *F. nobilis*, where an irregular mass of large cells is found.

In *F. subbasilaris* this type of costa can only be recognized in that part of the costa which does not have an epidermis of cells similar to those in the lamina.

Examined species: *F. adelphinus* Besch., Japan, Sasaoka 106 (U); *F. adianthoides* Hedw., France, St. Ceré, Bruggeman-Nannenga (Bruggeman-Nannenga); *F. allionii* Broth., Brazil, Reese 13.331 (U); *F. anomalus* Mont., Bhutan, Long 7868 (E, Bruggeman-Nannenga); *F. areolatus* Griff., Bhutan, Long 10577 (E, Bruggeman-Nannenga); *F. bushii* (Card. & Thér.) Card. & Thér., USA, Bruggeman-Nannenga 1119 (Bruggeman-Nannenga); *F. cadetii* Biz., La Réunion, Cadet 361 (PC-B); *F. dubius* P. Beauv., The Netherlands, Nannenga-Bremekamp 6 (Bruggeman-Nannenga); *F. geminiflorus* Doz. & Molkenb. var. *nagasakius* (Besch.) Iwats., Iwatsuki, Fiss. As. Exs. 2 (U); *F. glaucescens* Hornsch., South Africa, Vorster 14962 (L); *F. grandifrons* Brid., France, Bruggeman-Nannenga 1290 (Bruggeman-Nannenga); *F. javanicus* Doz. & Molkenb., Bhutan, Long 10576 (E, Bruggeman-Nannenga); *F. nigroviridis* Salm., Sarawak, Beccari 52 (PC, type); *F. nobilis* Griff., Iwatsuki, Fiss. As. exs. I: 5 (U); *F. nothotaxifolius* Pursell & Hoe, Hawaii, Hoe 1500 (PAC); *F. obscurus* Mitt., Bhutan, Long 8349 (E, Bruggeman-Nannenga); *F. osmundoides* Hedw., Labrador, Brassard 11707 (Bruggeman-Nannenga); *F. pacificus* Aongstr., Hawaii, Hoe 65A (PAC); *F. perdecurrens* Besch., Japan, Nochugi 102 (U) and Sasaoka 215 (U); *F. plagiochilus* Besch., Smith 8842 Fiji (U); *F. planifrons* Besch., Mayotte, Marie 160 (PC-B); *F. polyphyllus* Wils., Bruggeman-Nannenga 1357 (Bruggeman-Nannenga); *F. polypodioides*

Hedw., Jamaica, Jenman (U); *F. pulcher* C. Muell., Cameroon, Dusén 429 (PC-B, type); *F. serrulatus* Brid., Allorge, Bryoth. Iber. 19B (L); *F. subangustus* Fleisch., Iwatsuki, Fiss. As. exsicc. I: 7 (U); *F. subbasilaris* Hedw., USA, Ohio, Camus (PC-B); *F. taxifolius* Hedw., France, Hte Savoie, Bruggeman-Nannenga (Bruggeman-Nannenga); *F. teysmannianus* Doz. & Molk., Fleischer, Musc. Arch. Ind. II, 80 (U); *F. zippelianus*, Bhutan, Long 7746 (E).

III. **Bryoides-type** (Fig. 3a - c). This type differs from the previous 2 types in having only 3 (rarely more) large cells: two guide cells and one large central cell (Fig. 3b). The type is characterized by:

1) The presence of 2 guide cells.

2) One or more, large, central cells. When there is one it is between the two guide cells (Fig. 3b). When there are more one is between the two guide cells, and the other(s) is/are between this and the dorsal lamina (Fig. 3a).

3) Two lateral bands of small cells, which may have rather large lumina and thin walls, or may be substereids or stereids.

4) An epidermis which may or may not be differentiated.

5) Vaginant laminae which at their juncture with the costa are composed of laminal cells (Fig. 3a-b).

In as far as could be determined, the costa of the simple, upper part of the leaf has a single row of large cells (Fig. 3c).

In some species the costal tissue is so reduced that the structure described above can not be recognized, e.g. in *F. dummerii*. In the closely related *F. gladiolus*, however, it is recognizable in well developed parts of the costae.

Examined species:

Sect. *Aloma*: *F. calabariae* C. Muell., Tanzania, Pócs ca. 62571D (EGR); *F. celticus* Paton, Cornwall, Lostwithiel, Paton (Paton, Bruggeman-Nannenga); *F. cryptarum* C. Muell., Madagascar, Crosby 6700 (PC-B); *F. crassinervis*

Lac., Sumatra, Arens 576 (L) and Fleischer, Musci Frond. Arch. Ind. 17 (U); *F. flexinervis* Mitt., Surinam, Florschütz 2057 (U); *F. grandiretis* Ren. & Cardot, Madagascar, Sakana, Voeltz-Baur (H); *F. holstii* Broth. var. *perintegrifolius* Pot. Varde, Gabon, Lastourville, Le Testu (PC-PV, type); *F. kearnbachii* Broth., New Guinea, Robbins 2079; *F. linderii* Pot. Varde, Liberia, Linder 836 (PC-PV); *F. nitens* Salm. ex Rehm., Umpimilo, leg. Borgen (L); *F. pauperculus* Howe var. *pauperculus*, Surinam, Florschütz 2288 (U); *F. pellucidus* Hornsch., Puerto Rico, Bruggeman-Nannenga 46813 (U); *F. porrectus* Mitt., Niger-exp., Barter 1425 (NY) [NB. *F. porrectus* is limbate. It is included in the limbate sect. *Aloma* since it has smooth cells and a scariosus type peristome.]; *F. rivicola* Broth., Gabon, Le Testu 6842 (PC-PV); *F. sedgwickii* Broth. & Dix., Thailand, Touw 10788 (L); *F. splendens* Brugg.-Nann., Tanzania, Pócs 6285 (EGR).

Monopapillose species with a scariosus type of peristome: *F. brachypus* Mitt., Brazil, Buck e.a. 1798 (U); *F. donnellii* Austin, Guyana, Gradstein 4928 (U); *F. ghanæ* Biz., Ghana, Jones 1314 (PC); *F. gymnostomus* Brugg.-Nann., Brazil, Vital 5493 (SP, Bruggeman-Nannenga); *F. papillosum* Lac., Iwatsuki, Fiss. As. exs. II, 16 (U); *F. scleromitrius* (Besch.) Broth., Madagascar, Borgen (BM); *F. tenelliformis* Broth. & Watts, Lord Howe Island, Watts 221 (PC-Th).

Pluripapillose species with a scariosus-type of peristome (the peristome of *F. pseudoplumosus* is reduced, but the number of exothecial cells is that characteristic of taxa with a scariosus-type of peristome): *F. aoristoloma* Pot. Varde, Central African Republic, nr Mbaki, Tisserant (PC-PV); *F. erosulus* (C. Muell.) Par., Zimbabwe, Long 12475 (E, Bruggeman-Nannenga); *F. desertorum* (C. Muell.) Par., Nigeria, Ibadan Distr., Jones & Keay (PC); *F. foveolatus* Card., Bryoth. Naveau, Flora Congeana 540 (PC-Th); *F. glaucissimus* Welw. & Dub., Nigeria, MacFarlane 558 (PC); Central African Republic, Assel 722 (PC); *F. glaucopteris* C. Muell., Sierra Leone, Arnell 2391 (PC-PV) and Liberia, Dusén 99 (PC-PV); *F. glauculus* C. Muell., Nigeria, Verdoorn, Musc. Sel. Crit. VII, 321 (U); *F. humilis* Dix. & Watts, New South Wales, Streimann 5944 (L); *F. idanreensis* Pot. Varde, Mozambique, nr Inhaca, Péntek (EGR); *F. marthæ* Card., Oubangui, nr Donzo, Tisserant (PC-PV); *F. pseudoplumosus* Biz. & Onraedt, La Réunion, Onraedt 9378 (PC-B, type); *F. subelimbatus* Broth. & Pot. Varde, Oubangui, Gamburu, Tisserant (PC-Th); *F. sciophyllus* Mitt., Tanzania, Pócs 6188AJ (L); *F. weirii* Mitt., Cuba, Hioram 12842 (PC, type of *F. bizotii* Thér.);

F. wichuræ Broth. & Fleisch., Java, Meijer B 5780 (L).

Sect. *Areofissidens*: *F. cellulosus* Mitt., Tanzania, Pócs 6777A (Egr); *F. grandifolius* Broth. & Pot. Varde, Central African Republic, Faurel 10 (PC-B); *F. mollis* Mitt., Colombia, Griffin 11088 (L); *F. zollingerii* Mont., Fleischer, Musc. Frond. Arch. Ind. I, 14 (PC, as *F. xiphoides* Fleisch.).

Sect. *Fissidens* (*Nanobryum* included): *F. andicola* (Herz.) Brugg.-Nann., Bolivia, Herzog 199 (L); *F. androgynus* Bruch, Malawi, Long 12612 (E, Bruggeman-Nannenga); *F. attenuatus* Bryhn, Tenerife, Bryhn (PC); *F. bryoides* Hedw., Ireland, Bruggeman-Nannenga 1351 (Bruggeman-Nannenga); *F. crassipes* Wils. ex B.S.G., France, Bruggeman-Nannenga 415A (Bruggeman-Nannenga); *F. coacervatus* Brugg.-Nann., La Gomera, Schwab (Schwab, Bruggeman-Nannenga); *F. crenulatus* C. Muell., Brazil, Mosén 5 (H-Br); Mosén 128 (H-Br); *F. crispopachyloma* Dix., Tanzania, leg. Pócs 6208N (EGR); *F. curvatus* Hornsch., S. Africa, Rehm. 293 (L, type of its synonym *F. pycnophyllus* C. Muell.); *F. dietrichiae* C. Muell., Queensland, Bailey 235 (H); *F. diversifolius* Broth., India, Waistakhen, Sedgwick (L); *F. dummerii* (Dix.) Pursell & Reese, Uganda, Jones 572 (PC); *F. euryloma* Pot. Varde, Gabon, Mt Iboundji, Le Testu (PC-PV); *F. fluitans* (Pot. Varde) Brugg.-Nann., Gabon, Chute de la Lombo, Le Testu (PC); *F. gladiolus* Mitt. Central African Republic, Assel 416 (PC-B); *F. monguillonii* Thér., France, Bauer, Musc. Eur. Exs. 1028 (L); *F. ovatifolius* Ruthe, Italy, Lazio, Schwab (Schwab, Bruggeman-Nannenga); *F. pennula* Broth., Surinam, Florschütz-De Waard 5796 (U); *F. pungens* Hamp. & C. Muell., New South Wales, Streimann 7136 (L); *F. repandus* Wils., Colombia, Cleef 3731 (U) and 7978 (U); *F. rigidulus* Hook. f. & Wils. subsp. *rigidulus*, New Zealand, Poverty Bay, Sainsbury (BM) and Peru, Cook & Gilbert 670 (NY); *F. r.* subsp. *masatierrensis* Brugg.-Nann., Chili, Juan Fernandez Isl., Svensk. Pac. Exp. 1916-17: 63 (BM); *F. rivularis* (Spruce) B.S.G., Kreta, Gradstein & Smittenberg 1317 (U); *F. robynsianus* Pot. Varde, République Congo, Demaret 5257 (BR); *F. rochensis* Broth., Guadeloupe, Dusén 116 (H-Br); *F. rufulus* B.S.G., France, Bruggeman-Nannenga 419 (Bruggeman-Nannenga); *F. simensis* Schimp. ex C. Muell., Abyssinia, Schimper 1035 (PC); *F. strictulus* C. Muell., Japan, Iwatsuki, Fiss. As. exsicc. II, 17 (Bruggeman-Nannenga); *F. rufescens* Hornsch., South Africa, Schelpe 7529 (PRE); *F. steyermarkii* Bartr., Guatemala, Steyermark 36576 (FH); *F. ventricosus* Lesq., Oregon (PC-PV), *F. wallisii* C. Muell., Colombia, Van der Hammen 2794 (U) and Peru, Bues 1192 (NY).

Subg. *Octodicerias*: *F. fontanus* (B.-Pyl.) Steud., USA, Bruggeman-Nannenga 1085 (Bruggeman-Nannenga).

Subg. *Sarawakia*: *F. beccarii* (Hamp.) Broth., Sarawak, Beccari 30 (L); *F. hydropogon* Spruce ex Mitt., Andes Quitensis, Spruce 506 (NY); *F. stissotheca* (C. Muell.) Mitt. var. *stissotheca*, Brazil, Puiggari 1175 (H-Br) and Vital 2779-B (SP, Bruggeman-Nannenga); *F. s.* var. *immersus* (Mitt.) Pursell e.a., Brazil, Glaziou 2266 (H-BR) and Regnell, Pl. Brasil. Ser. III: 85 (H-BR).

Distribution of the costa types in the Fissidentaceae.

The bryoides-type of costa is found in taxa with a bryoides-type peristome (group Ia) and in taxa with a scariosus-type peristome (group Ib) (see Table I).

The differences in composition between groups Ia and Ib and the traditional supraspecific taxa have been discussed in Bruggeman-Nannenga and Berendsen (1988). A close relationship between the taxa forming group I is not only supported by the peristome, but also by costal structure.

The taxifolius-type of costa is found in sect. *Serridium*, in *F. grandifrons* (subg. *Pachyfissidens*) and in sect. *Crispidium*. It is also found in *F. allionii*, a monopapillose species with a scariosus-type peristome and a very stout costa. One would expect a bryoides-type of costa to be found in this species.

The oblongifolius-type of costa is found in sect. *Amblyothallia* and the fasciculatus group. On the basis of the peristome, the latter would appear to be more closely related to sect. *Serridium* (Group II). The oblongifolius-type is also found in *F. schusteri*, a semilimbate species with smooth cells and more than 40 exothelial cells (sect. *Fissidens*), which has a very strongly developed costa. In this species one would expect a bryoides-type of costa.

Remark. The distribution of the costa types given in table 1 applies to costae in the middle part of the vaginant laminae of vegetative leaves. Deviations from this scheme may occur in the basal part of the vaginant laminae of vege-

tative leaves and in perichaetial leaves, e.g. *F. wallisii* (sect. *Fissidens*) and *F. glaucissimus* (sect. *Pycnothallia*) have a bryoides-type costa in the middle part of the vaginant laminae, but a taxifolius-type in the basal part of the vaginant laminae. Vegetative leaves of *F. pseudoplumosus* (sect. *Semilimbidium*) have a bryoides-type of costa, but the perichaetial leaves have an oblongifolius-type. Deviations are also found in some, but not all, species with a strongly developed costa, e.g. in *F. allionii* and *F. schusteri* (see above).

It appears also (Table I) that:

- 1) Sect. *Crispidium* is characterized by a zippeianus-type peristome, more than 40 exothelial cells, and a taxifolius-type costa.
- 2) Subg. *Serridium* is characterized by a taxifolius- or nobilis-type peristome, more than 40 exothelial cells, and a taxifolius-type costa; the same combination is found in *F. grandifrons* Brid. (*Pachyfissidens*).
- 3) Sect. *Amblyothallia* is characterized by a similiretis-type peristome, more than 40 exothelial cells and an oblongifolius-type costa, whereas *F. fasciculatus*, *F. plumosus* and *F. asplenioides* (group fasciculatus) have a fasciculatus-type peristome, more than 40 exothelial cells, and an oblongifolius-type costa.
- 4) Subg. *Sarawakia*, subg. *Fissidens* sect. *Fissidens* and subg. *Nanobryum* are all characterized by a bryoides-type peristome, more than 40 exothelial cells, and a bryoides-type peristome.
- 5) Sect. *Areofissidens*, sect. *Aloma*, sect. *Crenularia*, sect. *Semilimbidium* and sect. *Pycnothallia* are all characterized by a scariosus-type of peristome, circa 32 exothelial cells, and a bryoides-type of costa.

It is now possible to distinguish two taxa that in the traditional way can not be separated very well, viz. subg. *Serridium* and sect. *Amblyothallia*. These two taxa are separated easily by their peristomes as well as by their costae. However, *F. pallidus* has an oblongifolius-type of costa and may have similiretis-type of peristome (both typical of sect. *Amblyothallia*), or it may have a peristome that in the undivided part has the characters of the taxifolius-type

peristome (typical of subg. *Serridium*), whereas the filaments are squamose as in the similiretis-type peristome.

Two other sections that are often confused, sect. *Amblyothallia* and sect. *Crispidium*, can be separated also by the type of costa and the type of peristome.

Note. During this study it became clear that, except for subg. *Serridium* the presence of a differentiated epidermis is diagnostic at the species level but not at the sectional level.

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