FISSIDENS SUBGENUS ALOMA (BRYOPHYTA) IN TROPICAL AFRICA I. THE LARGE-CELLED COSTATE AND ECOSTATE SPECIES

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Abstract. A revision of the large-celled costate and ecostate species of Fissidens subgenus Aloma Kindb. from tropical Africa is presented. Fissidens flaccidus var. mammillosus Brugg.-Nann. var. nov. is described and the Neotropical F. mollis Mitt. is reinstated. Most African specimens previously identified as F. enervis Sim are referred to Fissidens dealbatus Hook. f. & Wilson, a new indigene for Africa. Fissidens molliculus P. de la Varde, F. hedbergii P. de la Varde and F. hookerioides Bizot & Onr. in Bizot are subsumed under F. dealbatus. Fissidens enervis s.str. appeared to be a rare species. The distributions in O’Shea (2006) are revised, updated and, when necessary, amended. Fissidens flaccidus Mitt. is for the first time reported from South Africa and Guinea, F. zollingeri Mont. from Ghana, F. grandifolius Broth. & P. de la Varde from Cameroon and F. usambaricus Broth. from Malawi and Gabon. Pending further research, F. palmatus Hedw. is excluded from the African bryoflora. It is stressed that, since vegetative and perichaetial stems are different, perichaetial stems (and leaves of perichaetial stems) are to be compared with perichaetial stems (and leaves of perichaetial stems), whereas vegetative stems (and leaves of vegetative stems) should be compared with other vegetative stems (and leaves of vegetative stems).

Key words: distribution, Fissidens, large-celled Aloma, taxonomic revision, tropical Africa

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INTRODUCTION

Fissidens subgenus Aloma Kindb. embraces a wide range of gametophytic types (Pursell & Bruggeman-Nannenga 2004). Five not sharply distinct groups can be recognized: one without costa, one with large (over 30 µm long) cells, one with pluripapillose cells, one with unipapillose cells and one with smooth cells. Because of the existence of transitional species, these groups are no longer recognized as taxa (Pursell & Bruggeman-Nannenga 2004). Fissidens subgenus Aloma includes elimbate, semilimbate and a few completely limbate species, and the laminal cells are small, mediumsized or large. Ecostate species as well as species with large (30 µm long or more) laminal cells are restricted to this subgenus. A notable exception is the African F. subgenus Fissidens Hedw. species F. magnicellulatus Brugg.-Nann., which also has cells 30 µm long or more. This species is therefore included in the key below. All ecostate species have large cells but not all large-celled species are ecostate (Pursell & Bruggeman-Nannenga 2004). The present paper is a revision of those tropical African species of subgenus Aloma that have large (longer than 30 µm), smooth laminal cells. It includes both costate and ecostate species. In one species, F. zollingeri Mont., large cells are restricted to the vaginant lamina. With the exception of F. usambaricus Broth., all included species are limbane. Apart from their large cells, limbane, costate species bear a strong resemblance to subgenus Fissidens, which is characterized by limbane leaves and smooth laminal cells but has small to medium-sized cells and a different sporophyte.

This paper follows the classification by Pursell and Bruggeman-Nannenga (2004), who emphasized sporophytic characters. They considered large-celled limbane species to belong in subgenus Aloma, as they have Aloma sporophytes,¹ and classified limbane species with small, smooth cells 

¹ Capsule with ± 32 columns of exothecial cells and a scariosus-type peristome.

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in subgenus *Fissidens* because of their subgenus *Fissidens* sporophytes.\(^2\) Suzuki and Iwatsuki (2007, 2012), on the other hand, emphasized gametophytic characters. They classified ecostate species in subgenus *Aneuron* Kindb., and limbate, costate species with smooth cells, regardless of cell size and sporophytic characters, in subgenus *Fissidens*. It will be interesting to learn what fresh characters such as DNA will contribute to this question.

During this revision some challenging differences were found between the data in the monograph on Neotropical Fissidentaceae (Pursell 2007) and what is seen in Africa. Some of these have resulted in taxonomic decisions. A problem concerning *F. palmatus* Hedw. and *F. grandifolius* Broth. & P. de la Varde is discussed, but remains unsolved; hopefully this discussion will stimulate further research.

**Practical remarks**

It is self-evident that morphological taxonomic research needs to be based on comparisons of equivalent characters. In *Fissidens* the vegetative and perichaetial stems are different and have different leaves. Therefore, perichaetial stems (and leaves of perichaetial stems) are to be compared with perichaetial stems (and leaves of perichaetial stems), whereas vegetative stems (and leaves of vegetative stems) should be compared with other vegetative stems (and leaves of vegetative stems). In medium-sized and long stems all mid leaves have more or less the same shape and size. This makes such leaves most suitable for comparison. In short stems the leaf size increases rapidly up the stem, so comparison of these with leaves of longer stems will be problematic. One also needs to be cautious when comparing laminal cells. Nearness to the costa, the stem and the limbidium induces differentiation (cells become larger, more oblong and less ornamented). Moreover, whereas inner cells of the dorsal and apical lamina are similar, inner vaginant laminal cells tend to differ.

The ‘distributions’ in the present paper are supported by specimens examined for this paper or else their source is indicated. Distributions of some species are extended and/or had to be amended. No differentiation is made between the terms ‘mamillose’ and ‘unipapillose’. Trans-sections of these large-celled species are best examined in 5% KOH, which makes them swell beautifully.

**Key**

1. Leaves (±) ecostate .......................... 2
2. Leaves with distinct costa .................. 5
3. Leaves elimbate .......................... 4. *F. usambaricus*
2’. Leaves limbate .......................... 3
3’. Leaves mammillosus ...................... 3. *F. metzgeria*
3’. Limbidia narrower, ± 1 µm wide, limbidium distinct .................. 4
4. Capsule with 32 columns of exothecial cells, limbidia 1–2-stratose ........................ 2. *F. enervis*
4*. Capsule with 40 or more columns of exothecial cells, limbidia 1–7-stratose .......... 1. *F. dealbatus*
5. Mid dorsal laminal cells small, (6.5–)11.0–27.0 × 4.5–14.5(–19.5) µm ................... 9. *F. zollingeri*
5’. At least some mid dorsal laminal cells 30 µm or longer .................. 6
6. Costa ending well below apex ............ 7
6’. Costa reaching apex .................... 9
7. Laminal cells mammillosse .................. 5b. *F. flaccidus* var. *mammillosus*
7. Laminal cells smooth ....................... 8
8. Stems mostly short, palmate; capsules inclined; antheridia axillary and on tiny stems at base of perichaetial stems; limbidia weakly 1(-2)-stratose on mid dorsal lamina .......... 6. *F. grandifolius*
8’. Stems longer, with pinnately arranged leaves; capsules rare, erect; antheridia rare, terminal; limbidia stronger, (1-)2-stratose on mid dorsal lamina .................. 5a. *F. flaccidus* var. *flaccidus*
9. Limbidia not reaching leaf apex, intramarginal on all laminae .................. 8. *F. nigerianus*
9’. Limbidia reaching leaf apex, marginal on dorsal and apical lamina .............. 10
10. Leaves distant, peristome *bryoides*-type, ± 40 columns of exothecial cells on theca .......... 3. *F. magnicellulatus*
10’. Leaves crowded, peristome scariosus-type, ± 32 columns of exothecial cells on theca ........ 7. *F. minutifolius*

\(^2\) Capsule with 40 or more columns of exothecial cells and a *bryoides*-type peristome.

\(^3\) Not included in this paper. Description and figures in Bruggeman-Nannenga (2013a, b).
I. Ecostate species

Ecostate species represent a remarkable gametophytic group within subgenus Aloma, with large laminal cells and with central strands lacking or weakly developed. These species appear ecostate, yet many have or can have vestigial costae (Salmon 1899; Pursell & Bruggeman-Nannenga 2004) which occasionally can reach as far as the length of the vaginant lamina (e.g., in Miller Z215, F. usambaricus and the lectotype F. enervis Sim). Such weak costae have the same arrangement of cells as the bryoides-type costa with two large adaxial and one large central cell, but differ from well-developed bryoides-type costae in having thinner cell walls and absent or poorly developed lateral bands. Thus the ecostate species are not sharply distinct from the costate species. Ecostate species resemble costate subgenus Aloma species with large inflated cells. Many of these have costae that are short for the genus (Pursell & Bruggeman-Nannenga 2004). Like other subgenus Aloma species, ecostate species typically have capsules with ± 32 columns of exothecial cells and scariosus-type peristomes (Pursell & Bruggeman-Nannenga 2004).

It is interesting that not only the laminal cells but all or most gametophytic cells (e.g., cortical cells of the stem and cells of the calyptra) are inflated, whereas sporophytic cells are not. Limbidial cells are inflated in some species (e.g., Limbidial cells are inflated in some species (e.g., in Miller Z215, F. usambaricus and the lectotype F. enervis Sim)). Such weak costae have the same arrangement of cells as the bryoides-type costa having two large adaxial and one large central cell, but differ from well-developed bryoides-type costae in having thinner cell walls and absent or poorly developed lateral bands. Thus the ecostate species are not sharply distinct from the costate species. Ecostate species resemble costate subgenus Aloma species with large inflated cells. Many of these have costae that are short for the genus (Pursell & Bruggeman-Nannenga 2004). Like other subgenus Aloma species, ecostate species typically have capsules with ± 32 columns of exothecial cells and scariosus-type peristomes (Pursell & Bruggeman-Nannenga 2004).

Ecostate species can form dense mats but they frequently grow scattered among other mosses.

1. Fissidens dealbatus Hook. f. & Wilson


Fissidens hookerioides Bizot & Onr. in Bizot, Rev. Bryol. Lichénol. 42: 843. 1976 – PROTOLOGUE: MADAGASCAR, Tananarive, domaine des Frères de Soavimbafoaka, sur latèrite ombragée, 1400 m, 6 VII 1971, Onraedt 71/M/5137 (orthographic error) – label: as protologue except for the collection number which is 71/M/5137 (HOLOTYPE: PC-0096394!; ISOTYPE: BR!), syn. nov.

Stem in cross section without or with weakly developed central strand and 20–50 µm wide cortical cells, unbranched, with pinnately or, infrequently, elongated palmately arranged leaves, not heterocaulous, 1.5–3.0–6.5 × 1.0–3.0 mm, browning in KOH; rhizoids basal, colorless to pale brown, less often orange-brown, smooth; axillary nodules not differentiated; leaves typically distant, 6–10 leaf pairs, somewhat crispate when dry, elliptical with acute-acuminate or less often acute apex that ends in a narrow pointed cell, 0.9–2.3 × 0.2–0.6 mm, 2.5–5.0 times as long as wide, limbate; limbidium on all laminae, confluent at leaf apex, confluent at apex of vaginant lamina or not, reaching insertion of dorsal lamina, almost to completely reaching insertion of vaginant lamina, in mid dorsal lamina (4.5–)6.0–19.0 µm wide, 1–7-stratose (see remark below), marginal; on vaginant laminae 6.5–11.0 µm wide, 1–5-stratose, marginal; vaginant lamina 1/3–3/5 of leaf length, at insertion up to half as wide as stem, closed to ± closed, unistratose; dorsal lamina wide, tapering and straight to slightly rounded towards insertion, typically reaching insertion, not decurrent; dorsal and apical lamina unistratose, rarely with isolated,
unicellular bistratose dots; costa ± lacking, in surface view sometimes visible as differentiated band alongside vaginant lamina; mid dorsal laminal cells hexagonal, 22.5–77.0 × 16.0–33.5(–48.0) µm, smooth, plane to inconspicuously bulging; mid vaginant laminal cells narrower, 45.0–95.0 × 12.0–30.5 µm; no gemmae observed.

**Fertile parts, perigonia and perichaetia** terminal on separate plants in same collection. Perigonia terminal on 1.5–3.0 mm long perigonal plants; antheridia 210 µm long; perichaetia terminal, perichaetal leaves 1.5–2.6 mm long; archegonia 200–290 µm long; calyptra tightly clasping operculum, scabrose, 0.6–0.8 mm long. Sporophyte. Seta 4–6 mm long, smooth, 1 per perichaetium; capsule symmetrical, 0.90–1.00 × 0.40–0.55 mm, 40–64 columns of oblong exothecial cells; peristome scariosus-type (basal part and filaments observed), teeth 56–60 µm wide at base; operculum rostrate, 0.8–0.9 mm long; spores 9.5–13.5 µm diam., smooth.

**Fissidens dealbatus** is characterized by its thecae with 40–64 columns of exothecial cells (exceptionally high for subgenus *Aloma*), distinct, narrow, 1–7-stratose limbidia of narrow (lamina ± 1 µm wide) limbidial cells, ecostate leaves that are limbate on all laminae, and large laminal cells. The disparity between the large inflated laminal cells and the narrow limbidial cells in this species is striking. This is particularly clear in trans-sections (Fig. 1J, K–L). There is considerable variation in leaf shape and the length and width of the mid laminal cells. The type of *F. hookerioides* is a small expression with short, relatively wide leaves and ± isodiametric cells. **Fissidens dealbatus** is most likely to be confused with *F. hyalinus* (not known from Africa) and *F. enervis*; like *F. dealbatus*, these species have large cells, ecostate, limbate leaves, and marked contrast between the large inflated laminal cells and narrow limbidial cells.

**Fissidens dealbatus** differs from both in the number of columns of exothecial cells (40 or more versus ± 32) and thicker limbidia (unistratose in *F. hyalinus* – *fide* Iwatsuki & Suzuki 1995 and 1–2-stratose in *F. enervis*). Furthermore, *F. dealbatus* and *F. hyalinus* have acute to acute acuminate leaf apices, whereas *F. enervis* has cuspidate ones. Many collections of this species are too small to make trans-sections of them, and capsules are often lacking. In such cases one has to resort to estimating the thickness of the limbidium, which is unreliable. The third ecostate, limbate African species, *F. metzgeria*, is easily distinguished by its ill-defined limbidium of wide cells and the frequent occurrence of characteristic, multicellular, epilaminal gemmae.

**Remarks.** Previously, *F. molliculus* (Bizot & Pócs 1979) and *F. hedbergii* (Bruggeman-Nannenga 1997) were considered to be *F. enervis*. Most specimens were re-examined during the preparation of the present paper. Many specimens earlier identified as *F. enervis* appeared to differ from that species by having limbidia thicker than 1–2 layers and in having 40 or more columns of exothecial cells (versus ± 32 in *F. enervis*). Of the African material studied, only the type specimen could be retained in *F. enervis*. Comparison of tropical African collections with acute-acuminate apices, 40 or more columns of exothecial cells and pluristratose limbidia with *F. dealbatus* from New Zealand and Guadalcanal showed the African collections to be conspecific with *F. dealbatus* Hook. f. & Wils.

No trans-sections were made of the type of *F. hookerioides*. Its limbidia were estimated to be pluristratose. Sporophytes were lacking.

In *F. dealbatus* the limbidia often ‘fold’ around the laminal cells and then are not truly pluristratose (e.g., Fig. 1L, which in the present paper has been interpreted as 7-stratose).

![Fig. 1. Fissidens dealbatus Hook. f. & Wilson. A – perichaetial plant, B & C – leaves, D & E – leaf apices, F – insertion of leaf, G – capsule and calyptra, H – trans-section of stem, I – trans-section of leaf with unistratose laminae, J – trans-section of dorsal lamina with bistratose dot, K & L – trans-sections of vaginant lamina limbidia (K with 1–2-cells wide, 2–4-stratose limbidium; L with one-cell-wide, 7-stratose limbidium) – A, F, J from Pócs 9104/P; B, D, G–I, K, L from Müller B98; C from Pócs 8430A; E from Townsend 75/330.](image-url)
SUBSTRATE AND HABIT. On soil, rarely on rocks, once on soil-covered wood. Growing scattered among other mosses or less often in pure mats.

HABITAT. In all kinds of forests (montane rainforest, montane cloud forest, montane evergreen forest, mesic montane forest, submontane rainforest, bamboo forest); also collected in Philippia heath with remnants of montane evergreen forest and in a Eucalyptus plantation.

ELEVATION. In Africa known from 950–2500 m a.s.l.; in New Zealand from 0–900 m a.s.l. (Beever et al. 2002).

DISTRIIBUTION. Fissidens dealbatus is widespread in tropical Africa. West tropical Africa (Bioko), west central tropical Africa (Central African Republic), east tropical Africa (Kenya, Rwanda, Tanzania, Uganda), south tropical Africa (Malawi) and western Indian Ocean (Madagascar).

Outside Africa it is known from New Zealand, New Caledonia, Australia (Beever et al. 2002) and the New Hebrides (Iwatsuki & Suzuki 1995).

Also recorded (as F. enervis) from the Democratic Republic of the Congo (O’Shea 2006), São Tomé and Príncipe (Shevock et al. 2013) and Zambia (O’Shea 2006). These are not included in the distribution since they may refer to F. dealbatus. A specimen from South Africa [Transvaal, Ofcolaco, Brenan M 3280A (E)] seems to be this species, but the material is too poor for certainty.

SELECTED SPECIMENS EXAMINED: CENTRAL AFRICAN REPUBLIC, type F. molliculus. – EQUATORIAL GUINEA, Bioko, 10 km S of Luba, Berg Caldera, 3°22′N, 8°32′E, Müller B98, p.p. (DR, L). – MADAGASCAR, type F. hookerioides. – KENYA, Rift Valley Province, Trans Nzoia District, Cherangani, R.A. Maas Geesteranus 10313a (L, a few stems). – MALAWI, S Escarpment of Zomba Plateau on the S slope of Kuchawe summit, Pöcs 9171/BD (EGR, L, a few mixed with F. rotereaui P de la Varde). – RWANDA, Lac Bulera (au nord-est de Ruhengiri), rive nord du Lac, De Sloover 13.565, p.p., a few mixed with several other Fissidens species (L, a few stems). – TANZANIA, Nguru Mountains in Morogoro District, watershed between Chogowale and Divue headwaters, 6 km SSE of Maskati village, Kis & Pöcs 9129/Q (EGR, L); West Usambara Mts, E of Magila village, SW edge of Ndelemi F.R., Pöcs 8430/A (EGR, L); Arusha National Park, E slopes of Meru Crater, along trails between Kitoto and Cabin at Njeku, 3°14′S, 34°47′E, Crosby & Crosby 11231 (MO, L); Mt. Meru, SW slope of Mt. Meru above Laikinio, Pöcs & Ochyra 88147/H (EGR, L). – UGANDA, Kibale NP, Research Forest, MUBFS, Kanyawara, 0°33′N, 30°21′E, Wigginton U 5285A (E, L, a few mixed with Fissidens intramarginatus s.l. and a few F. zollingeri); Kisoro, Fitzgerald s.n. (PC). – NEW ZEALAND, North Island, South Auckland Land District, Te Kauri Scenic Reserve, 38°4′0″S, 174°59′0″E, Spragg 93 (AK, L). – GUADALCANAL, near camp at base of Mt. Popemanaue, Van Zanten 682582 (GRO, L).

ILLUSTRATIONS: Beever et al. (2002: 28; 2014: fig. 10), Bruggeman-Nannenga (2006a: fig. 7a–c, as F. enervis), Chuah-Petiot (2003: fig. 30, as F. enervis, but the shape of the apex indicates F. dealbatus rather than F. enervis), Salmon (1899: figs 13–15), Stone (1986: fig. 3), Seppelt & Stone (2016: F. dealbatus).

2. Fissidens enervis Sim

Stem in cross section without central strand (based on Indian specimen), unbranched, with pinnately arranged leaves (only fertile stems seen), ± 3.0 × 1.0–2.5 mm; rhizoids basal, from lower stem cortex and from apical part of lamina, hyaline or brown, smooth; leaves distant, to 7 pairs, crissate when dry, elliptical with cupulidise tip, 0.95–1.70 × 0.25–0.40 mm, 3.5–5.0 as long as wide, limbate; limbidium ± confluent at leaf apex, confluent at apex of vaginant laminae, reaching insertion of dorsal lamina, in upper leaves ending well above insertion of vaginant lamina, in lower

![Fig. 2. Fissidens enervis Sim. A – sporophytic stem, B – perigonial stem, C – leaf apex, D – detail of leaf apex with rhizoid growing from lamina, E – mid leaf, F – insertion of leaf, G – limbidium on mid dorsal lamina, H – capsule. All from type specimen.](image-url)
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leaves sometimes reaching insertion, in mid dorsal lamina 7.5–14.5 μm wide, more than unistratose (estimated); on vaginant lamina, 20 μm wide, 1–3-stratose (based on Indian specimen), marginal throughout; vaginant lamina ca 1/2 of leaf length, at base less wide than stem, slightly rounded at insertion, not decurrent, unistratose, subequal; dorsal lamina ± straight towards insertion, reaching insertion, not decurrent, dorsal and apical lamina unistratose; costa lacking or vestigial, composed of narrow cells, reaching to half the length of vaginant lamina, lacking in lower leaves (no cross sections seen); mid dorsal laminal cells plane, 32–67 × 15–30 μm; mid vaginant laminal cells large, plane, 51.5–54.0 × 18.5–25.5 μm. Gemmae, some leaves produce rhizoids from apical part (Fig. 2 D).

Fertile parts. Perigonía terminal on small, ca 1.5 mm long, stems; antheridia 230–250 μm long; perichaetial terminal, perichaetial leaves ± 1.3 mm long; archegonia not seen; calyptra not seen. Sporophyte, seta ± 4 mm long, smooth, 1 per perichaetium; capsule symmetrical, 0.5–0.7 × 0.25–0.40 mm, ± 32 columns of quadrate-oblong exothecial cells; peristome scariosus-type, tooth base ± 33.5–43.0 μm wide; operculum and spores not seen.

Fissidens enervis is a rare species known from a few small collections. It is characterized by its cuspidate leaf apex, (±) ecostate leaves and large laminal cells. Rhizoids (hyaline, green or brown) growing from laminal cells are frequently present (seen in the type specimen as well as in Indian specimens). It strongly resembles F. hyalinus (not known from Africa). These two species may eventually prove to be conspecific. In this paper I take a conservative stand and consider specimens with unistratose limbidia and acute to acute-acuminate leaf apices to be F. hyalinus, and specimens with 1–2-stratose limbidia and cuspidate apices to be F. enervis. In Africa Fissidens enervis has been confused with F. dealbatus (see under this species). Sporophytic specimens are clearly distinct. Fissidens enervis has a smaller number of columns of exothecial cells (32 versus 40 or more in F. dealbatus). Gametophytic stems differ in the shape of the leaf apex (cuspidate in F. enervis and acute to acute-acuminate in F. dealbatus) and in having thinner limbidia (limbidia of F. dealbatus are 1–7-stratose). Rhizoids growing from laminal cells are present in all known collections of F. enervis but have not been observed in F. dealbatus. Unfortunately, capsules are frequently lacking and the collections are often too small to make trans-sections. In such cases the thickness of the limbidium is estimated from a surface view, which is unreliable.

Remarks. The lectotype of F. enervis consists of a few poor stems, including one sporophyte with ± 32 columns of exothecial cells on the theca.

Fissidens splachnoides Broth. is very similar. Its type (Queensland, Indooroopilly, F.M. Bailey 256, p.p. (H-BR) also has a cuspidate leaf apex (Stone 1986, fig. 2) and 1–2-stratose limbidia. However, in this species the walls of the lateral bands of the vestigial costae are thickened [observed in the type specimen Bailey 256 (SI!), in Norkett 16173 (BM!) and in New South Wales, Watts 5624 (H-Broth!)], which is not the case in an Indian specimen of F. enervis.

Substrate & Habit. On soil, growing scattered among other mosses.


Distribution (amended). Southern Africa (South Africa), Russia? (Ignatov et al. 2007), India (Western Ghats). Rare.

To the extent that it could be checked, the African distribution of F. enervis in O’Shea (2006) refers, with the exception of the type specimen, to F. dealbatus. The F. hyalinus with 1–2-stratose limbidia and cuspidate apices in Ignatov et al. (2007) seems to refer to F. enervis.

Specimens examined. SOUTH AFRICA, lectotype (PRE); Natal, Nottingham Road, 900 m, IV 191, Van de Bijl (Sim 8648) (PRE). – INDIA, Kerala, Palakkad District, Nelliampathi; on land cuttings, 1200 m, 13.07.2015, K.M. Manjula 1138B (CALI, L).


Fig. 3  


*Fissidens bryum* Müll. Hal. ex Dusén, Kongl. Svenska Vetensk. Acad. Handl. n.s. 28(2): 14, figs.: a, b & tab. II, f. 8. 1895 – PROTOLOGUE: CAMEROON [Camerunia], supra Bomanam pagum, c. 1100 m, VII 1892, Dusén s.n. – HOLOTYPE: Africa Occ., Camerunia in monte Camerun, ca. 1100 m, VII 1892, Dusén s.n. (S!); ISOTYPE label: Kamerun, Bomana, 1100 m, auf Steinen, VII 1892, Dusén 834 (PC-PV!).


Stem without or with weak central strand, not heterocaulous, with pinnately arranged leaves, unbranched, 5.0–21.0 × 1.5–5.0 mm, browning in KOH or not; rhizoids basal and from cortex of basal part of stem, brown, smooth; axillary cells not differentiated; leaves shiny, distant to close, up to 15 pairs, slightly crispate when dry, flattening when moistened, elliptical to elliptico-lanceolate with acute to acute-acuminate apex, 1.5–4.0 × 0.3–0.7 mm, 3.0–5.5 times as long as wide, margin entire to undulate-entire, limbate; limbidium on all laminae of all leaves, ill-defined, lax, ± reaching apices of leaf and vaginant lamina, reaching insertions of vaginant and dorsal laminae, in mid dorsal lamina 10.5–33.5 µm wide, unistratose, marginal; on vaginant laminae weak, up to 56 µm wide, unistratose, marginal to weakly intramarginal; vaginant lamina 1/2 (–3/5) of total leaf length, about half as wide as stem at insertion, slightly open, unistratose; dorsal lamina tapering towards base, straight, reaching insertion, not to inconspicuously decurrent; dorsal and apical lamina unistratose, infrequently with scattered, unicellular bistratose dots; costa lacking, rarely weakly developed; mid dorsal laminal cells oblong-hexagonal, 55.0–120.0 × 15.0–53.5 µm, plane to inconspicuously convex, smooth; limbidial cells in mid dorsal lamina 130–150 × 5–12 µm with slightly thicker walls than inner cells; mid vaginant laminal cells oblong-rectangular 75–152 × 5–24 µm. Clusters of gemmae frequently present on lamina, particularly near apex, less often growing from stem cortex; gemmae brown, unbranched to heavily branched, multi-cellular.

Fertile plants rare, perigonal and perichaetial stems hardly differ from vegetative ones, easily overlooked. Perigonia, perichaetia and synoicia terminal; perigonal plants up to 6 mm long, antheridia 210–500 µm long; perichaetia terminal, perichaetal leaves hardly longer than stem leaves, 1.5–4.0 mm long, archegonia 200–450 µm long; calyptra tightly clasping operculum, 0.65–0.70 mm long, smooth to scabrose. Sporophytes (only 2 very young ones seen), 2 per perichaetium.

*Fissidens metzgeria* is characterized by its ecosiate, limbate leaves, ill-defined limbidia, 5–12 µm wide limbidial cells and large inflated cells (55.0–120.0 × 15.0–53.5 µm in mid dorsal lamina). Epiphyllous clusters of multicellular gemmae are frequently present on the apical part of the leaf. The other two African ecosiate, limbate species, *F. enervis* and *F. dealbatus* and *F. enervis*, have distinct, narrower limbidia of narrow limbidial cells and lack epiphyllous clusters of gemmae. *Fissidens ecuadorensis* Pursell & Brugg.-Nann. is a smaller (stems up to 4 mm long) Neotropical ecosiate species with a similar ill-defined limbidium.

Substrate and habit. On soil, less often on rocks, living or dead wood. Often scattered among other mosses, rarely in mats or tufts.

Habitat. On banks of paths, roads and streams in humid, shady to swampy sites and also near waterfalls. In all kinds of forest (montane and submontane rainforest, montane cloud forest, dry semi-deciduous forest, swamp forest, both pristine and secondary).

Elevation. 360–2300 m a.s.l.
DISTRIBUTION. Endemic to Africa. Known from west tropical Africa (Guinea; Schultze-Motel 1975, Nigeria), west central tropical Africa [Cameroon, Central African Republic, Democratic Republic of the Congo, Equatorial Guinea (Bioko), Gabon, São Tomé], northeast tropical Africa (Ethiopia; Hylander et al. 2017), east tropical Africa (Kenya, Rwanda, Tanzania, Uganda) and south tropical Africa (Angola; Müller 2015).


ILLUSTRATIONS: Potier de la Varde [1929: 3, and (same figure) 1936: 3; both as F. bryum]; Bruggeman-Nannenga (2006a: fig. 7d–f).

4. Fissidens usambaricus Broth. Fig. 3


Stem without or with weak central strand, not heterozaeous, mostly unbranched, 3.0–9.0(–15.0) × 1.5–3.0 mm, with pinnately arranged leaves; rhizoids basal, infrequently from mid stem cortex, brown to hyaline; axillary cells not differentiated; leaves green, distant, 5–15 pairs, hardly altered to crispate when dry, broadly elliptical to broadly elliptico-oblongate or oblong with widely acute to obtuse or rounded-obtuse apex, 0.9–1.5(–2.1) × 0.4–0.6(–0.7) mm, 2–3 times as long as wide, elimate, margin subentire, near apex sometimes serrulate; vaginant lamina 2/5–3/5 of total leaf length, narrow, at insertion narrower than stem, slightly unequal, unistratose, infrequently with scattered unicellular bistratose dots; dorsal lamina

Fig. 3. Fissidens metzgeria (Müll. Hal.) Broth. A – stem, B–F – leaves (black areas are clusters of gemmae), G – leaf apex with 3 clusters of gemmae, H – limbidium mid dorsal lamina, I – insertion of leaf, J – cluster of gemmae, K – trans-section of stem, L – detail of K showing weak central strand, M & N – trans-sections of leaf (M showing isolated bistratose dot in dorsal lamina), A from Pocs 90099/AA; B–D from Hodgetts U4254A; E, G–H, K–N from Müller B104; F, J from Müller B410; I from O’Shea U 5532A.
± straight towards insertion, reaching insertion, occasionally decurrent, unistratose, rarely bistratose near insertion; apical lamina unistratose; costa ± absent; mid dorsal laminal cells hexagonal, variable in size (see remark below), 22.5–93.0 × 14.0–40.0 μm, smooth, plane to inconspicuously convex; marginal cells smaller, isodiametric to oblong, on the mid dorsal lamina 15.0–33.5 × 6.5–15.9 μm; mid vaginant laminal cells hardly differentiated to larger, 45.0–136.0 × 7.5–32.0 μm; basal vaginant laminal cells hardly differentiated to oblong, 45.0–60.0 × 7.5–14.5 μm. No gemmae seen.

Fertile parts. Gametangia (perigonia, perichaetia and synoicia) terminal; perigonial stems 0.5–2.3 mm long; antheridia 180–230 μm tall; perichaetial and synoicial stems 3–5 mm tall; archegonia ± 300 μm long; perichaetial leaves 1.85–2.20 mm long; calyptra tightly covering rostrum, smooth to slightly bulging. Sporophytes rare. Seta 1.5–3.0 mm long, 1–2(–3) per perichaetium, smooth or slightly scabrose in basal half; capsule symmetrical, rarely slightly inclined, 0.40–0.65 × 0.20–0.45 mm, with ± 32 columns of oblong to quadrate exothecial cells with thickened corners; peristome scariosus-type, tooth base 45–48 μm wide; operculum rostrate, 0.55 mm long; spores subglobose, 8.0–13.0 μm diam., thick-walled or not, smooth to indistinctly papillose.

This species is easily recognized by its elimbate, (±) ecostate leaves and large laminal cells with a border of 1–2 rows of smaller, isodiametric to oblong cells. The variation of cell size in this species is remarkable. Some collections have relatively small, 22.5–45.0 × 14.0–21.0 μm, mid dorsal laminal cells, whereas others have much larger, 56–80 × 30–40 μm, mid dorsal laminal cells (e.g., O’Shea 2628A and Müller Z 215); mid vaginant laminal cells can be 45–60 × 7.5–14.5 μm in some collections or as large as 88–136 × 17.5–32 μm in others. The presence of transitional forms makes it impossible to distinguish distinct groups based on this character. *Fissidens usambaricus* is the only elimbate, ecostate species known from Africa. The ecostate *F. hylogenes* Dixon from New Zealand similarly has elimbate leaves but has smaller, ± 12 × 9 μm (versus 15.0–24.0 × 7.5–15.0 μm) marginal cells and crenulate instead of subentire margins. [Specimen seen: Sainsbury et al., Musci exsiccati. Novae-Zelandiae 10 (S)].

**Substrate and habit.** Mostly on soil, less often on rock, termite mounds or wood. Growing scattered among other mosses, rarely in loose or dense mats or tufts. Easily overlooked.

**Habitat.** Usually collected on shady banks and road cuts, also found near a waterfall, on rock in streamlet and bank of stream. Known from dry semi-deciduous forests, mesic montane forests and rainforest (lowland, submontane and montane), also from an Afro-montane forest, woodbush, and from *Pinus* plantations. Many labels give no details.

**Elevation.** 25–2400 m a.s.l.

**Distribution.** A widespread African endemic. Known from Macaronesia: Cape Verde Islands (O’Shea 2006), west tropical Africa (Ivory Coast; O’Shea 2006), Nigeria (O’Shea 2006), west central tropical Africa (Cameroon; O’Shea 2006), Central African Republic, Democratic Republic of the Congo, Gabon, Rwanda, Sāo Tomé (Shevock et al. 2013), northeast tropical Africa (Ethiopia), east tropical Africa (Kenya; O’Shea 2006), Tanzania, Uganda, south tropical Africa (Malawi) and southern Africa (South Africa, Swaziland; O’Shea 2006). New for Malawi and Gabon.

**Selected specimens examined:** CENTRAL AFRICAN REPUBLIC, types of *Fissidens chevalieri*. – DEMOCRATIC REPUBLIC OF THE CONGO, prov. Kivu: Ruwenzori, Lanuri, Bequaert 4447 (PC, PC-PV, BM); Kahuzi-Biega Nat. Park. Surroundings of Camp Biega 30 km W of Bukavu. Loc. 128, Bryotrop Exp. 1991, Pöcs 7356, p.p., 1 stem (L); Pinga, 96 km NW

Fig. 4. *Fissidens usambaricus* Broth. A & B – sporophytic plants, C – mid leaf of perichaetial stem, D & E – leaf apices, F – margin mid dorsal lamina (marginal cells at right), G – insertion of leaf, H – part of seta showing large cortical cells, I – capsule with calyptra. A from Pöcs 90096/AA; B, C from Porley U45A; D, H from Hylander 4527; E, G from Porley 410A; F from Porley U636A; I from Lübenau SA309.

ILLUSTRATIONS: Bruggeman-Nannenga (2006a: fig. 7 g–i), Chuah Petiot (2003: fig. 35), Magill (1981: fig. 8–13), Salmon (1899: fig. 16).

II. Costate species

All species included in the present paper have large (at least 30 µm long) laminal cells, limbidia on all laminae of all or most leaves, and a subgenus Aloma sporophyte. Costae are frequently short for the genus (e.g., F. flaccidus, F. grandifolius) but can be excurrent, as in F. minutifolius Broth. & P de la Varde and F. zollingeri Mont. Worldwide, costate species with large leaves include limbidia, partly limbate and ± elimbate species. Most have smooth cells but a few have mammillose cells (e.g., F. flaccidus var. mammillosus Brugg.-Nann., F. lindbergii A. Jaeg., F. yucatanensis Steere, F. biformal Mitt.). In F. zollingeri (smooth cells) and F. biformal Mitt. (with mammillose cells, not included in this paper), large inflated cells are restricted to the vaginant laminae.

5. Fissidens flaccidus Mitt.


Non-African synonyms:


Fig. 5. Fissidens flaccidus Mitt. var. flaccidus. A – vegetative stem, B & C – perichaetial stems, D–F – leaves, G–H – leaf apices, I – mid dorsal lamina, J – insertion of leaf, K – trans-section of leaf showing bryoides-type costa, L – clusters of axillary gemmae, M – 2 gemmae. – F. flaccidus var. mammillosus Brugg.-Nann., var. nov. N – mammillae in side view, O – mid dorsal laminal cells. A from Pócs 9168/O; B from Pócs 9168/Q; C, H from type F. ensifolius; D, M from Pobeguin 306; E, K from Miller E194; F from Dorr 2752; G, I, from Pócs 9168/P; J from MacFarlane 811; L from McFarlane 168; N, O from type specimen of F. flaccidus var. mammillosus.


5a. F. flaccidus var. flaccidus  Fig. 5A–M

Stems without or with weak central strand, browning in KOH, hardly heterochaetous, mostly unbranched; vegetative stems 1.4–13.0 × 0.7–4.0 mm (sporophytic/perichaetial stems 5–10 × 2–3 mm); rhizoids basal and from stem cortex, pale to dark brown, smooth; axillary nodules not differentiated; leaves pinnately, less often frondosely arranged, distant, less often close, 5–15(–32) pairs, strongly crispate to hardly altered when dry, usually flattening in 5% KOH, elliptical, elliptico-lanceolate and elliptico-oblancoate with acute to acute-acuminate apex ending in pointed colored cell, (0.6–)0.8–2.8 × 0.10–0.70 mm, 3.5–7 times as long as wide; limbidium on all laminae of all well-developed leaves, reaching leaf apex, often becoming weak towards leaf apex (Fig. 5G), occasionally confluent into ecostate macro (Fig. 5H), confluent at apex of vaginant laminae, mostly reaching insertion of dorsal lamina, on vaginant lamina often becoming lax and indistinct proximally and reaching insertion or not, on mid dorsal laminae 8–21(–27) μm wide, 1–2-stratose, marginal; on mid vaginant lamina (11.0–) 14.5–27.0 (–50.0) μm, 1–2-stratose, near insertion marginal or weakly intramarginal; vaginant lamina 1/2–3/5 of leaf length, at base less wide than stem, frequently slightly decurrent (best visible with KOH; Fig. 5J), unistratose, ± closed; dorsal lamina narrow, straight to slightly rounded at insertion, reaching insertion, not decurrent; dorsal and apical lamina unistratose; costa ending 7–21 cells below leaf apex, in cross section of bryoides-type; mid dorsal laminal cells (18.5–)23.0–50.0(–65.0) × 8.0–25.5(–28.0) μm, smooth, plane to lowly convex; mid vaginant laminal cells oblong, 26.5–76.5(–80.0) × 7.0–24.0(–30.0) μm; juxta-costal cells of vaginant lamina 44.0–58.0(–72.0) × 9.5–18.0 μm; axillary fascicles of short rhizoids bearing multicellular, uniseriate, hyaline to brown gemmae (Fig. 5L & M) often present.

Fertile parts, perigonia and perichaetia on separate plants, perigonal plants 2–3 mm long, hardly differentiated and easily overlooked, perigonia terminal, antheridia ± 250 μm long; perichaetia terminal on plants or, less often, on branches; perichaetal leaves longer than stem leaves (1.3–)1.7–3.0 mm long; archegonia 200–380 μm long; calyptra not seen. Sporophyte, seta 2–5 mm long, smooth, 1 per perichaetium; capsule erect, 0.50–0.65 × 0.35–0.45 mm with ca 32 columns of quadratic-oblong, exothelial cells with thickened corners; peristome scariosus-type (only basal part seen), tooth base 54.5–56.5 μm wide; operculum long-rostrate, 0.5 mm long; spores 12.5–18.0 μm diam., finely papillose.

Fissidens flaccidus var. flaccidus is characterized by its completely limbate leaves, (1–)2-stratose limbidia, smooth, large cells (in mid dorsal lamina, at least some 30 μm or more long), short costa ending 7–21 cells below the leaf apex, and (0.6–)0.8–2.8 mm long leaves. Multicellular gemmae on short, axillary rhizoids are often present. Archegonia are frequently present but sporophytes are rare. Variability. Typically the laminae are unistratose and the limbidia 1–2-stratose. Müller E 201 is a robust expression in which all laminae have unicellular bistratose dots and the limbidia are 1–2-stratose near the insertion of vaginant laminae. Fissidens flaccidus var. flaccidus is most likely to be confused with F. grandifolius, which differs by having inclined capsules, 1–4 setae per perichaetium, axillary perigonial buds and dwarf male plants at the base of perichaetal stems (terminal in F. flaccidus). The few sporophytic plants of F. flaccidus observed [type-specimen of F. bocarangerensis; Stone (1988) as F. maceratus; Eddy (1988) as F. atroviridis] have 1 seta per perichaetium and erect capsules. Whereas sporophytic collections of the two species are easily distinguished, this is not true for vegetative collections. However, though both species have 1–2-stratose limbidia (in one and the same leaf), limbidia of F. flaccidus are essentially bistratose, whereas those of F. grandifolius
are more often unistratose. Furthermore, though their cell sizes overlap, cells of *F. grandifolius* are typically somewhat larger (mid dorsal laminal cells (28.0–)34.5–71.0(–77.0) × 12.5–37.0 µm versus (18.5–)23.0–50.0(–65.0) × 8.0–25.5(–28.0) µm in *F. flaccidus*); moreover, gemmae are common in *F. flaccidus* but have not been observed in *F. grandifolius*. The Namibian *F. capriviensis* Magill (not seen) is corticolous, has weaker limbidia and is smaller in all respects (Magill, 1981). The minute *F. minutifolius* has longer costae which reach the leaf apex. The South African species *F. wageri* Dixon and *F. splachnifolius* Hornsch. similarly have large cells and short costae, but are easily distinguished by their elimbate leaves (Magill, 1981). Outside Africa, *F. flaccidus* resembles the Neotropical *F. dissetifolius* Sull. that differs by having shorter limbidia which end below the leaf apex and having smaller laminal cells [(13.9–)18.0–29.0(–36.0) × 9.0–16.0(–22.0) µm; Pursell 2007].

**Fissidens flaccidus, F. mollis and F. maceratus.** *Fissidens mollis*, a species from the Neotropics, was considered conspecific with *F. flaccidus* by Bruggeman-Nannenga and Pursell (1995). During the present study it appeared that the African specimens, including the type specimen of *F. flaccidus*, differ essentially from Pursell’s (2007) diagnosis by having thinner limbidia [(1–)2-stratose rather than 2–4-stratose] and shorter leaves (up to 2.8 mm versus up to 5.0 mm long). Moreover, whereas in the Neotropics the costae vary between ending as many as 18 cells below the leaf apex to percurrent (Pursell 2007), the costae of African collections always end well below the apex. Neotropical specimens agreeing with Pursell’s diagnosis (long leaves and thick limbidia confluent at the apex) include the type specimen of *F. mollis*. Therefore this species is here reinstated. Both species have limbate leaves and large cells, and frequently have axillary, multicellular gemmae. *Fissidens flaccidus s.str.* is also known from the Neotropics (for an example see examined specimens). Its distribution in the Neotropics is unknown. *Fissidens maceratus* Mitt. was correctly subsumed under *F. flaccidus* (Pursell 1997).

**Substrate and habit.** On rock (unspecified, limestone, travertine, walls) and soil. Once collected on a termite mound. Growing in mats, tufts or scattered, often sparsely intermixed with other species and then easily overlooked.

**Habitat.** mostly in forests [lowland rainforest (7×), riverine forest (6×), also in moist semi-deciduous rainforest, submontane rainforest, evergreen forest, mixed low-elevation hardwood forest, secondary low-elevation tropical hardwood forest with palms, and degraded, dry forest], also collected in Sudano-Guinean savanna, plantations and gardens. Frequently growing near water [stream banks, near waterfalls, irrigated limestone (travertine bank), man-made walls of ditches, swimming pools, etc.], occasionally submerged.

**Elevation.** 0–1800 m a.s.l. (based on African collections).

**Distribution.** Widespread and common in Africa. Macaronesia (Cape Verde Islands); west tropical Africa (Ghana, Guinea, Ivory Coast, Niger, Nigeria, São Tomé, Sierra Leone); west-central tropical Africa (Central African Republic); east tropical Africa (Tanzania, Uganda); south tropical Africa [Angola (Müller 2015), Zambia, Zimbabwe (O’Shea 2006)]; southern Africa (South Africa) and western Indian Ocean (Comoro islands, Madagascar, Mauritius, Réunion, Rodriguez, Seychelles, Socotra; O’Shea 2006). Outside Africa known from Brazil, Asia, Australia and Oceania. New for Guinea and South Africa.

**Specimens examined: CAPE VERDE ISLANDS, Brava, an der Strasse zum Flughafen, Lindlar 95 (BONN). – CENTRAL AFRICAN REPUBLIC, Bamingui-Bangoran, Parc de Manovo-Gounda-Saint Floris. Campement de Koubamba, 8°30’S, 21°13’E, Prendergast 91 (PC, L); Bocaranga, sur la route Bocaranga-Kounnang près village Zöl, Eckendorff s.n. (L). – COMOROS, Ndzuani (Anjouan) Island, NW coast near Ouani, near Hotel Guinguette, Pöcs 9168/K, M, O, Q (all EGR, L); collapsed Crater of Mt Pamouni on the S end of the island, E of M’rijou village, 12°20’21”S, 44°29’57”E, Pöcs, Magill & Rupf 9281/G (EGR, L); Ngazidja (Grande Comore) Island, Ikoni Town on the West Coast below the volcanic cliffs at the fort hill, Pöcs 9148/B, p.p. a few stems (EGR, L). – GHANA, Ashanti Region, Bobiri Forest reserve; 6.41˚N 1.20˚W, Jouko 040001-64 with F. ramulosus (H, L). – GUINEA, Djallon-Timbo, Pobeguin 306 a few stems (L). – IVORY
COAST, Man, Cascade de Man 4 km W of Man; 7°25′S, 7°35′W. F. Müller E 201 (L, DR); – MADAGASCAR, prov. Antananarivo, Antananarivo, Parc de Tsimbazaza, 18°55′S, 47°31′E, L.J. Dorr 2752 (MO, L a few stems among F. androgyrus); Mahamasina, ouest de Tanararive, Imerina, Camboué s.n. (PC). – MAURITIUS, Cave near Bassin Anglais, Curepipe.

5b. *F. flaccidus* var. *mammillosus* Brugg.-Nann., *var. nov.*

**Diagnosis.** The new variety differs from var. *flaccidus* by its mammilllose (low-conical with inconspicuously thickened apical area) laminal cells. The mammillae are best observed in leaf folds or in surface view. In cross section they are hard to observe. The new variety resembles the smaller *F. lindbergii* Mitt. from Central and northern South America. Stone (1988) described and figured a similar-looking *Fissidens* from Queensland without naming it, but the mammillae in her figure do not have a thickened apex.

**SUBSTRATE, HABIT AND HABITAT.** In tuft on wall of culvert in deep shade; semiaquatic (covered by diatoms).

**DISTRIBUTION.** African endemic. Sierra Leone, known from the type locality only.

6. *Fissidens grandifolius* Broth. & P. de la Varde **Fig. 6**

*in* P. de la Varde, Bull. Soc. Bot. France 73: 57, f. 25.1. 1926 – PROTOLOGUE: [GABON], sur terre argileuse. Rive gauche de la Ngounyé, entre Udendé et Labo, XII 1924, *Le Testu 5346 – LECTOTYPE (nov.)* with label: Rive gauche de la Ngounyé entre Udendé et Labo, en forêt, sur argile, 29 10-bri 1924, *Fissidens* from Queens-land without naming it, but the mammillae in her figure do not have a thickened apex.

**Stem** without or with weak central strand, mostly unbranched; vegetative stems, frondose to elongate-frondose, variable in size, (1.5–)2.5–5.0 × 1.0–4.0 mm, unbranched; sporophytic stems taller,
4–8 × 3–5 mm, with frondosely to pinnately arranged leaves; rhizoids basal and from stem cortex, brown to hyaline, smooth; axillary nodules not developed; leaves close, less often distant, 4–9 pairs, shriveled and crispate when dry, not well flattening in water, flattening in 5% KOH, elliptical, ellipsoid-lanceolate to elliptico-oblanceolate with acute to acute-acuminate apex, ending in large pointed cell, limbate, in vegetative stems (1.0–)1.6–3.2 × 0.3–0.7 mm, 3.5–6.5(–7.5) times as long as wide; in sporophytic stems 3.3–3.9 × 0.5–0.6 mm, 5.5–7.8 times as long as wide; limbidium on all laminae of all well-developed leaves, confluent at leaf apex, often becoming weak towards leaf apex, confluent at apex of vaginant laminae, becoming weak towards insertion of vaginant lamina, reaching or ± reaching insertion of dorsal lamina; in mid dorsal lamina 11–32 µm wide, 1(–2)-stratose, marginal, on vaginant laminae (13–)16–43 µm wide, 1(–2)-stratose, marginal to weakly intramarginal; vaginant lamina 1/2–3/5 of leaf length, at base narrower than stem, closed to ± closed, unistratose; dorsal lamina narrow, straight to slightly rounded at base, reaching insertion, not decurrent, dorsal and apical lamina unistratose; costa ending 10–26 cells below leaf apex, weak in upper part, in lower leaves not always exceeding length of vaginant laminae, in cross section bryoides-type; mid dorsal laminal cells hexagonal, large, variable (28.0–)34.5–71.0(–77.0) × 12.5–37.0 µm, smooth, plane to inconspicuously convex; mid vaginant laminal cells (30.0–)40.0–110.0 × 10.0–32.0 µm, smooth, plane; basal vaginant laminal cells oblong, 69.0–114.0 × 12.0–29.0 µm; gemmae not observed.

Fertile parts, perigonia and perichaetia on same stem, perigonia frequent, terminal on axillary, stalked (Fig. 6 I, J), budlike, 0.3–0.7 mm long (including stalk) branches and on tiny plants at base of perichaetial plants; antheridia 150–180 µm long; perichaetium terminal, perichaetal leaves (1.8–)3.3–4.0 mm long, archegonia 150–300 µm long; calyptra 0.7 mm long, smooth. Sporophyte, seta 5–10 mm long, smooth, 1–4 per perichaetium; capsule oblique, small, 0.4–0.6 × 0.2–0.35 mm, with ca 32 columns of exothecial cells with strongly thickened corners; peristome scariosus-type, tooth base 50–54 µm wide; operculum 0.5 mm long (immature); spores subglobose, 9.0–14.5 µm long, faintly papillose.

Fissidens grandifolius is characterized by its limbate leaves, large cells, and 1–4 setae per perichaetium, inclined capsules, stalked axillary perigonal buds and dwarf male plants at the base of perichaetial stems. The limbidia are uni- to bisтратose. There are typically ± 32 columns of exothecial cells, but sometimes more, due to extra cell divisions on one side of the capsule. The species is highly variable in size and cell size. Sporophytic stems tend to be taller and have longer leaves than vegetative ones, and more often have pinnately arranged leaves. A small expression was identified by Shevock et al. (2013) as F. palmatus. Based on the available material it seemed impossible to demonstrate a sharp distinction between small and large expressions. Fissidens grandifolius can also be confused with F. flaccidus. For differences see under the latter.

Fissidens palmatus and F. grandifolius. Both F. palmatus and the African F. grandifolius display two expressions. As indicated above, the African F. grandifolius has large and small expressions which are not sharply separated. Pursell’s (2007) concept of Neotropical F. palmatus is broad and includes F. palmatus Hedw. s.str. with percurrent costae as well as expressions with costae that end well below the apex. The latter used to be known as F. reticulosus (Müll. Hal.) A. Jaeger in the Neotropics. Small non-sporophytic expressions of the African F. grandifolius resemble the F. reticulosus expression; indeed, one specimen was reported as F. palmatus by Shevock et al. (2013). The two species may prove to be conspecific in future but the situation is complex. It seems significant that F. palmatus s.str. is unknown from Africa, whereas the large expression of F. grandifolius is restricted to West Africa. In contrast to F. palmatus in the Neotropics, F. grandifolius has sporophytic plants that tend to be taller and to have longer leaves, (3.3–3.9 mm versus up to 2.8 mm long) and more setae (1–4 per perichaetium, versus 1–2). There may be differences in cell size as well, but this could not be established as it is not clear.
which cells were measured for the Neotropical monograph. More material from both continents is needed for taxonomic decisions. Pending this, the collection from São Tomé earlier reported as *F. palmatus* (Shevock et al. 2013) is here tentatively included in *F. grandifolius*.

**Substrate and Habit.** On soil and wood. Growing in mats or scattered among other mosses.

**Habitat.** Often not indicated, forest including a riverine forest.

**Elevation.** Sea level to 230 m a.s.l.

**Distribution.** Endemic to West Africa. Known from west tropical Africa (Guinea; O'Shea 2006; Liberia, Nigeria, Sierra Leone, Togo; O'Shea 2006) and west central tropical Africa (Cameroon, Central African Republic, Gabon, São Tomé). Not common. New for Cameroon.

Also reported from Ivory Coast (Müller & Schäfer-Verwimp 1999) but this specimen appeared to be *F. flaccidus*.


**Fig. 6.** *Fissidens minutifolius* Broth. & P. de la Varde


**Stem** frondose, unbranched, 1.0–1.7 × 1.5 mm (only fertile plants seen); **rhizoids** numerous, basal and from stem cortex, hyaline, ± smooth; **leaves** close, 3–8 pairs, crispate when dry (impossible to revive without KOH), elliptico-lanceolate to oblanceolate, acute-acuminate ending in pointed cell, 1.0–1.2 × 0.2–0.3 mm, 4–6 times as long as wide, limbate; **limbidium** on all laminae of all well-developed leaves, reaching leaf apex and fusing with costa, confluent at apex of vaginant laminae, becoming weak towards insertion of vaginant laminae, ± reaching insertion of dorsal lamina, in mid dorsal laminae 18 µm wide, 1–2-stratose (estimated), marginal; on vaginant lamina 22.5 µm wide, lax, marginal; **vaginant lamina** 1/3–2/3 of leaf length, at base about as wide as stem, almost closed; **dorsal lamina** narrowing towards insertion, reaching insertion, not decurrent; **costa** ex- to percurrent; **mid dorsal laminal cells** hexagonal, 30.0–52.5 × 15.0–18.0 µm, smooth; **mid vaginant laminal cells** up to 60 µm long. No **gemmae** seen.

**Fertile parts,** **perigonia** numerous, terminal on short, ± 0.35 mm long, bud-shaped plants at base of female plants, **antheridia** not seen; **perichaetia** terminal, **perichaetal leaves** 1.5–1.7 × 1.5 mm, **archegonia** not seen; **calyptra** not seen. **Sporophyte,** seta 3.5–5.0 mm long, smooth, 1 per perichaetium; **capsule** erect to slightly inclined, 0.5 × 0.45 mm, with ca 32 columns of oblong exothelial cells with strongly thickened corners; **peristome** scariosus-type, **teeth** at base 33.0–40.5 µm wide; **operculum**
long-rostrate, 0.6 mm long; spores 9–12 µm long, smooth.

This tiny species is characterized by its frondose stems, over 30 µm long laminal cells, completely limbate leaves, per- to excurrent costae, a scariosus-type peristome and ± 32 columns of exothecial cells on the capsule. It can be confused with *F. flaccidus*, which is larger and has shorter costae, and with *F. zollingeri*, which has half as large mid dorsal laminal cells. *Fissidens minutifolius* further resembles the subgenus *Fissidens* species *F. aciphyllus* Dixon and *F. magnicellulatus* Brugg.-Nann., which both differ in having a higher number of exothecial cells (40 columns or more) and a bryoides-type peristome. *F. aciphyllus* Dixon and *F. magnicellulatus* Brugg.-Nann. are very similar; and it cannot be ruled out that *F. magnicellulatus* will prove to be a perichaetial expression, with relatively large cells, of *F. aciphyllus*.

**Remarks.** Due to the paucity of the available material, no cross sections were made. Features that can only be observed when leaves are removed (e.g., axillary nodules) are also excluded from the description.

**Habitat, substrate and habit.** In forest on soil. Sparsely scattered among *F. grandifolius* plants, covered with dirt.

**Elevation.** Not indicated.

**Distribution.** A rare species, known from west-central tropical Africa (Gabon). Further reported from west tropical Africa (Togo and Nigeria O’Shea 2006).

**Specimens examined:** GABON, types (PC-PV, H-BR); Pétsyalango, Le Testus n.n. (PC-0705948, PC-PV).

**Illustration:** Potier de la Varde (1926: f. 25, 2; 1936: f. 4, 2 – same figure as 1926).

8. *Fissidens nigerianus* Bizot ex Brugg.-Nann.  


**Fig. 7. Fissidens minutifolius** Broth. & P. de la Varde. A – sporophytic stem, B – 3 young perichaetial stems, C – base of sporophytic stem with attached dwarf perichaetial and perigonal stems, D – leaf, E & F – leaf apices, G – mid leaf, H – bifurcation of peristome tooth showing upper part of basal undivided part and basalt part of two filaments. All from lectotype.

No vegetative stems observed, probably heterochoasms, perichaetial stems 0.60–1.50 × 0.45–1.50 mm, unbranched, frondose; persistent filamentous protonema well developed; rhizoids basal, hyaline to pale brown, smooth; axillary nodules weakly differentiated; leaves imbricate, 2–5 pairs, slightly crispate when dry, lanceolate, acuminate-mucronate (perichaetial leaves), 0.7–1.6 × 0.15–0.3 mm, 3.5 times as long as wide, margins limbate, serrate where eliminate, limbidia frequently intramarginal on all laminae, extension and occurrence variable, typically present on all laminae, in perichaetial leaves not or ± confluent at apex of vaginant laminae and ± reaching leaf apex or ending well below it, in lower leaves less developed; often becoming ill-defined towards insertion of vaginant lamina; reaching insertion of dorsal lamina or ending well above it, in mid dorsal lamina 19 µm wide, unistratose (estimated), marginal or intramarginal; on vaginant laminae 16–24 µm wide, unistratose (estimated), marginal or intramarginal by one row of cells; vaginant lamina 3/5 of leaf length, at base narrower than stem, unistratose, slightly open; dorsal lamina tapering towards insertion, in perichaetial leaves reaching insertion to ending well above, not decurrent; dorsal and apical lamina unistratose; costa long excurrent in perichaetial leaves, per- to long excurrent in lower leaves; mid dorsal laminal cells hexagonal, large, 25.0–38.5 × 13.0–21.5 µm, smooth, plane; mid vaginant laminal cells oblong-hexagonal, 25.5–70.5 × 11.5–24.0 µm, smooth, plane. *Gemmae* 150 × 25 µm, monosericate, growing from persistent protonema.

**Fertile parts, perigonia** terminal on small, ± 0.4 mm tall plants at base of perichaetial plants; antheridia ± 100 µm long; perichaetia terminal; perichaetial leaves 0.7–1.2 mm long; archegonia ± 180 µm long; calyptra 0.4 mm long, smooth.
**Sporophyte, seta** 3.0–4.5 mm long, smooth, 1–2 per perichaetium; **capsule** ± erect, 0.40–0.50 × 0.25–0.35 mm, with ca 32 columns of oblong exothecial cells; **peristome** details not observed, tooth base 41.5 µm wide; **operculum** rostrate, 0.45 mm long; **spores** subglobose, 11–13 µm long, smooth.

This species is known from the type collection only. It is characterized by its limbate leaves with limbidia that are often intramarginal on all laminae, per- to excurrent costae, large cells (in mid dorsal lamina 25.0–38.5 × 13.0–21.5 µm), and persistent protonemata with gemmae. Though intramarginal limbidia on vaginant lamina are fairly common in the Fissidentaceae, intramarginal limbidia on the dorsal and apical lamina are much rarer and thus have diagnostic value. *Fissidens minutifolius* thus have diagnostic value.

**Remark.** Due to the paucity of the available material, no cross sections were made.

**Substrate and habitat.** Scattered on worm casts in deep shade in forest.

**Elevation.** 520 m a.s.l.

**Distribution.** Nigeria, known from the type locality only.

**Specimen examined:** type specimen.

**Illustration:** Bizot (1974: pl. 1A, 1–2).

**9. Fissidens zollingeri** Mont.  

**Fissidens vogelianus** Mitt., Trans. Linn. Soc. London 23: 54, t. 5, f. 10. 1860 – **Protologue:** RIVER NIGER, Vogel – **type label:** Africa, Niger-expedition, Vogel s.n. (HOLOTYPE NY, ISOTYPE PC); **isotype:** BM as Vogel 3.


**Fissidens platybryoides** Müll. Hal. in Flora 69: 505. 1886 – **Protologue:** [NIGERIA], Africa occid. Tropica, Old Calabar, in territorio fluminis Niger, in terra, 10 XI 1884, Mönkemeyer s.n. – **LECTOTYPE** (designated by Bruggeman-Nannenga 1997) with label: Niger Gebiet, Alt Calabar, in terra, 11 (sic!) X 1885 (sic!), Mönkemeyer s.n. (H-BR); **ISOLECTOTYPE** labeled: Afr. Occ. Old Calabar, in terra, 10 1885, Moenkemeyer s.n. (PC).

**Fissidens tenuisetus** Cardot, Rev. Bryol. 35: 64, 1908 – **Protologue:** DEMOCRATIC REPUBLIC OF THE CONGO, [Congo belge], Kisantu, sur la terre et le bois pourri, H. Vanderist (sic!), 1906 – **TYPE** label: Congo belge, Kisantu, 1906, Vanderijst (sic!) s.n. (HOLOTYPE: PC!; **ISOTYPE:** H-BR).


Stem without or with weak central strand, hardly heterocalous, unbranched to frequently branched, 2.4–5.0 × 1.7–3.5 mm; rhizoids basal and from basal stem cortex, brown, smooth; axillary nodules differentiated or not; leaves frondosely to pinnately arranged, crowded to distant, 3–12 pairs, crispate when dry, elliptical to elliptic-lanceolate or obovate-lanceolate with acute to acute-acuminate to mucronate apex, (1.1–)1.5–2.5(–3.0) × 0.2–0.5 mm, 3.0–6.0(–7.5) times as long as wide, limbate on all laminae of all leaves; limbidia reaching leaf apex, often becoming indistinct at apex or sometimes ending below it, confluent at junction of vaginant laminae, reaching insertion of vaginant lamina, reaching insertion of dorsal lamina or ending slightly above, in mid dorsal lamina 6–19 µm wide, (1–)2-stratose; on vaginant laminae 15–40 µm wide, 1–2(–3)-stratose, marginal to weakly intramarginal near insertion; vaginant laminae 1/5–2/3 of leaf length, at base narrower than stem, closed, unistratose; dorsal laminae tapering below, straight to slightly rounded at base, reaching insertion or not, not decurrent; dorsal and apical lamina unistratose; costa percurrent to long-excurrent, bryoides-type; mid dorsal laminar cells hexagonal, variable in size (6.5–)11.0–27.0 × 4.5–14.5(–19.5) µm, smooth, plane; mid vaginant laminar cells hexagonal to oblong, (10.0–)14.0–36.5 × (5.0–)9.0–16.0(–18.5) µm; basal vaginant laminar cells oblong, (18–)34.5–81(–94.5) × (6.5–)10.5–24.5(–31) µm. Gemmae on short axillary rhizoids, uniseriate multicellular, once in terminal cluster on short stalks, 0.6–0.7 × 0.1 mm, rare.


Fertile parts. Perigonia and perichaetium on separate stems or on same stem, synoicia rare; perigonia terminal on 0.85–3.00 mm long stems, also on budlike, 0.6–1.1 mm long branches; antheridia 120–300 µm long; perichaetium terminal on stems and/or branches; perichaetial leaves slightly longer than stem leaves, 1.1–3.0 mm long; archegonia 200–400 µm long; calyptra 0.6–0.8 mm long, smooth. Sporophyte, seta 3.5–6.5 mm long, smooth, 1–2 per perichaetium; capsule erect to suberect, 0.40–0.90 × 0.20–0.45 mm, with ca 32, oblong or quadrato-oblong exothecial cells with thin walls and thickened corners; peristome scarious-type, tooth base 33–53 µm wide; operculum rostrate, 0.55–0.80 mm long; spores (7.0–)9.0–14.5 × (5.0–)8.0–12.5 µm, papillose to smooth.

Fissidens zollingeri is a heterogeneous species. Features common to all specimens are the limbidia on all laminae of all leaves, per- to excurrent costa, smooth, medium-sized laminal cells, and when sporophytes are present ± 32 columns of exothecial cells around the capsule. The combination of this last character with limbate leaves and smooth, medium-sized cells is rare in the Fissidentaceae. Stems can be short and frondose with imbricate leaves, but collections with longer stems and pinnately arranged leaves are not rare. The juxta-costal cells of the vaginant laminae are typically large and clear (usually easily visible at 5× magnification) and conspicuously inflated (Fig. 9D, H, I); hyaline axillary nodules are present or not. In the majority of specimens the limbidia reach the leaf apex and the insertion of the dorsal lamina, but in a fair number the limbidia become weak towards the leaf apex or end below it and/or end above the insertion of the dorsal lamina. Mid dorsal laminar cells vary in size at (6.5–)11.0–27.0 × 4.5–14.5(–19.5) µm. Cell size differs greatly between specimens. In most specimens the mid dorsal laminar cells are ± 16 µm long, but collections with smaller or larger cells (though always less than 30 µm) are regularly found. Specimens with small cells
include, for example, *Pócs 8436/AA* (mid dorsal laminal cells 6.5–11.5 × 5.0–8.0 µm) and *Dilg I–3* [mid dorsal laminal cells (6.0–)9.0–11.5(–12.5) × (5.0–)6.0–8.5(–10.0) µm]. Larger plants tend to have larger cells and – rather surprisingly, because typically large plants have better-developed limbidia – more often have elimate leaf apices, but this correlation is weak. The African *F. minutifolius* resembles frondose specimens of *F. zollingeri* in having limbate leaves, per- to excurrent costa and smooth laminal cells, but it has larger, 30.0–52.5 × 15.0–18.0 µm, mid dorsal laminal cells. *Fissidens zollingeri* can further be confused with *F. biformis* Mitt. (= *F. angustifolius* Sull.), which is distinct with its mammillose laminal cells, and with species of subgenus *Fissidens*. With the latter it shares laminate leaves and smooth laminal cells, but species of subgenus *Fissidens* have sporophytes with 40 or more columns of exothecial cells around the theca, and also *bryoides*-type peristomes. In tropical Africa the subgenus *Fissidens* species with which *F. zollingeri* is most likely to be confused is *F. curvatus* Hornsch. Apart from the differences in sporophytic characters, this species is distinct from being heterocaulous (that is, having vegetative stems that differ markedly from shorter perichaetial ones).

**SUBSTRATE AND HABIT.** Most often on soil, frequently on rocks, rarely on wood (twigs, wood and bark) or termitic mounds. Growing in mats, small tufts, or scattered.

**HABITAT.** On shady road edges and stream banks in forests (lowland and montane rainforests, once in semi-deciduous forest, once in riverine forest), less often in savannas or cultivated areas (plantations, gardens, etc.). Frequently found in wet places (near rivers, springs and cascades), occasionally submerged.

**ELEVATION.** In Africa 0–1750(–2100) m a.s.l.; in the Neotropics up to 3360 m a.s.l. (Pursell 2007).

**DISTRIBUTION.** Common and widespread. African distribution: west tropical Africa (Benin, Gambia, Ghana, Guinea, Ivory Coast, Nigeria, São Tomé and Príncipe); west-central tropical Africa (Cameroon, Democratic Republic of the Congo, Central African Republic, Gabon); east tropical Africa (Kenya; Kis 1985; Tanzania, Uganda); south tropical Africa (Angola, Zambia; Kis 1985) and western Indian Ocean (Comoro islands, Madagascar, Réunion, Rodriguez, Seychelles). New for Ghana. Outside Africa known from the Neotropics, Asia and Oceania.

lane 254 (L, private herbarium McFarlane); Div. Akure, Richards 3808 (PC-PV). – RÉUNION, Anse des Cascades, 21°10’S, 55°50’E, Bruggeman-Nannenga 11014 (L, REU). – RODRIGUEZ, Balfour s.n. (NY). – SÃO TOME & PRINCIPE, Island of Principe, below roça Belo Monte Resort, Lat/Long NAD 83: 01°41′13.1″N, 07°26′34.8″E, Shevock et al. 49767 (L, mixed between *F. grandifolius*). – SEYCHELLES, MAHÉ, path near Botanical Gardens, Norkett 16880 (BM); banks of La Misère Road, Norkett 17025 (BM, L); PRASLIN, path near Grande Anse, Norkett 18349 (BM). – TANZANIA, Dar es Salaam University campus by Mulakwa stream course, above University Road. Wingfield 2776A (MO); Morogoro Mts, N valley of Lupanga, behind Kigurunyembe Missin and TTC, 6°50.4′S, 37°42′E, Pócs 97220/A, p.p. mixed with *Fissidens* specs. (EGR, L); Nguru Mts in Morogoro District, Mt Kanga N of Tu-riani, Pócs 90110/L (EGR a few mixed with *F. crispulus* Brid.); East Usambara Mts, around Amani Medical Research Center, Pócs 87115/N (EGR, L); West Usambara Mts, forest in entrance of gorge of the SW escarpment, above Mazinde village, Pócs 8436/AA, AG (EGR, L). – UGANDA, Hoima District, Itohya Forest, 1.5 km SW of Muntene village, 25 km WSW of Hoima Town. 1°18.2′N, 31°3.4′E., Lye & Pócs 97120/O (EGR); Mpanga Forest Reserve, Kampala, Jones 600 (E, BM, L, cum spor.); Mpigi, Mpanga Forest Nature Reserve, 0°12′N, 32°18′E, Wigginton 2004-2 A (E, L); Masindi District, Budongo Forest, near Sonso, 1°43′N, 31°31′E, Wigginton 2004-2 A (E, L); Kabarole, Kibale Forest, Kanyawara (S), 0°33′N, 30°21′E, Bates U 8644A (E, L).


**Type Material Not Available for Study**


The protologue is of a species with large cells, limbate leaves, and costae ending far below the apex. It is excluded since the type could not be located.

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**References**


