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On the peristomes of the corticolous African species of *Fissidens* Hedw. (Fissidentaceae, Bryophyta)

Maria Alida BRUGGEMAN-NANNENGA
Griffensteijnseplein 23
NL-3703 BE Zeist (The Netherlands)

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ABSTRACT
The peristomes of 18 corticolous African *Fissidens* Hedw. species are described in detail and illustrated with light microscope images. Seventeen belong to *F.* subgen. *Polypodiopsis* sect. *Antennidens* and one to *F.* subgen. *Neoamblyothallia*. Most of these peristomes are imperfect. Compared to their presumed ancestral types, they are shorter, narrower, stiffer, undivided, deeply divided or irregularly divided, and in having a reduced hygroscopic capacity. Other sporophytic traits frequently found together with these anomalous peristomes are: narrow, cylindrical capsules with narrow, oblong exothecial cells; short and often papillose setae; and short opercula. Based on literature a strong relation is demonstrated between a corticolous life-style and anomalous peristomes for *F.* subgen. *Polypodiopsis* and *F.* subgen. *Neoamblyothallia*, whereas in the type subgenus anomalous peristomes are often connected with an aquatic habitat.

KEY WORDS
Africa,
Fissidentaceae, Bryophyta,
Fissidens,
corticoles,
anomalous peristomes.

RÉSUMÉ
Sur les péristomes des espèces corticoles africaines de Fissidens *Hedw. (Fissidentaceae, Bryophyta).*
Les péristomes de 18 espèces africaines corticoles de *Fissidens* Hedw. sont décrits en détail et illustrés par des images au microscope optique. Dix-sept appartiennent à *F.* subgen. *Polypodiopsis* sect. *Antennidens* et une à *F.* subgen. *Neoamblyothallia*. La plupart de ces péristomes sont imparfaits. Par rapport à leurs types ancestraux présumés, ils sont plus courts, plus étroits, plus rigides, non divisés, profondément divisés ou irrégulièrement divisés, et ont une capacité hygroscopique réduite. D'autres caractéristiques sporophytiques sont fréquemment trouvées avec ces péristomes anormaux : des capsules étroites et cylindriques avec des cellules exothécales étroites et oblongues ; des setae courtes et souvent papillaires ; et des opercules courts. En se basant sur la littérature, une relation forte est démontrée entre un style de vie corticole et des péristomes anormaux pour *F.* subgen. *Polypodiopsis* et *F.* subgen. *Neoamblyothallia*, alors que dans le sous-genre type les péristomes anormaux sont souvent liés à un habitat aquatique.

MOTS CLÉS
Afrique,
Fissidentaceae, Bryophyta,
Fissidens,
corticoles,
péristomes anormaux.

INTRODUCTION

When identifying *Fissidens* Hedw. for the MadBryo project (https://www.madbryo.org/) I was struck by the large number of anomalous peristomes found in corticolous species. This led to the present morphological study of the peristomes of corticolous African *Fissidens* species.

The genus *Fissidens*

The Fissidentaceae are a large cosmopolitan, monogeneric family. They are named for their peristome teeth which are divided into two filaments, *Fissidens* meaning "split tooth". Suzuki *et al*. (2018) in a phylogenetic study divided the family into three subgenera. However, the last word on the infrageneric classification has not yet been written and refinements are to be expected when more molecular data become available.

The infrageneric classification of *Fissidens* has been discussed by Kindberg (1898), Müller (1901), Brotherus (1901, 1924), Pursell & Bruggeman-Nannenga (2004), Suzuki & Iwatsuki (2007) and in the molecular study by Suzuki *et al*. (2018). The phylogenetic tree of Suzuki *et al*. (2018) (based on chloroplast rbcL and rps4 genes of 50 species of *Fissidens*) supports parts of all traditional classifications, i.e. those of Brotherus (1901, 1924), of Pursell & Bruggeman-Nannenga (2004) and of Suzuki & Iwatsuki (2007). Some subgenera and sections included in Suzuki *et al*. (2018), e.g. *F.* subgen. *Pachyfissidens, F.* subgen. *Fissidens* and *F.* subgen. *Polypodiopsis* sect. *Antennidens* (as clade *Semilimbidium*) are well represented in that study, although most type species were not included. Other taxa were represented by a few species only or not at all (sect. *Pynothalllia*). Results for "*Aloma*" in their phylogenetic tree were a surprise. Two well-known traditional *F.* sect. *Aloma* species were resolved in quite different clades. *Fissidens pellucidus* Hornsch. in *F.* sect. *Antennidens* (as clade *Semilimbidium*) and *F. exilis* Hedw. in the clade that Suzuki *et al*. (2018) indicate as "sect. *Aloma*". The morphological characterization of this clade is unclear. *Fissidens exilis* is morphologically well defined, but the other two species in this clade have strongly reduced stems. Suzuki *et al*. (2018) hypothesize that the type species of *Aloma* (*Fissidens pauperculus* Howe) belongs to this clade. Should this assumption prove to be correct, the name for this clade would be *Aloma.*

It is clear that when more molecular results become available the infrageneric classification of *Fissidens* will need to be amended. In this paper I follow in part the classification of Suzuki *et al*. (2018) and in part that of Pursell & Bruggeman-Nannenga (2004). Thus, I treat clade "sect. *Polypodiopsis* + sect. *Areofissidens* + sect. *Aloma* + sect. *Semilimbidium*" (Suzuki *et al*. 2018) as a subgenus of the same rank as subgen. *Fissidens*, viz. subgen. *Polypodiopsis*, instead of as a complex section. All but one of the species in the present paper belong to subgen. *Polypodiopsis* sect. *Antennidens* (Müll.Hall.) Paris.

The main peristome types in *Fissidens*

Five main types of peristomes are recognized in the Fissidentaceae, each diagnostic for a subgenus or section. The *taxifolius*-type is characteristic for *F.* subgen. *Pachyfissidens*; the *similiretis*-type for *F.* subgen. *Neoamblyothallia* sect. *Neoamblyothallia*; the *zippelianus*-type for *F.* subgen. *Neoamblyothallia* sect. *Crispidium*; the *bryoides*-type for *F.* subgen. *Fissidens*; and the *scariosus*-type for *F.* subgen. *Polypodiopsis* (Pursell & Bruggeman-Nannenga 2004; Suzuki *et al*. 2018; Bruggeman-Nannenga 2021). Based on the exterior side of the undivided part of the peristome tooth, these main types can be divided into two groups. The *taxifolius*-type, the *zippelianus*-type and the *bryoides*-type have high trabeculae and a low lamellar ornamentation; while the *similiretis*- and the *scariosus*-type have a high, horizontal lamellar ornamentation that is about as high as the trabeculae (Pursell & Bruggeman-Nannenga 2004). When one follows the taxa characterized by these character-states in the phylogenetic tree of Suzuki *et al*. (2018) it appears that low papillose lamellae are pleisiomorphic and that a high lamellar ornamentation has evolved twice, once when *F.* subgen. *Neoamblyothallia* sect. *Neoamblyothallia* branched off and again when *F.* subgen. *Fissidens* and *F.* subgenus *Polypodiopsis* were separated. The *scariosus*- and *bryoides*-type and *F.* subgen. *Polypodiopsis* are discussed and illustrated by Bruggeman-Nannenga (2021). The largest number of plesiomorphic character states is found in the *taxifolius*-type (Suzuki *et al*. 2018).

The present paper is a morphological study. Therefore, I cannot presume to answer questions about the evolutionary processes that have led to the development of these anomalous peristomes, nor why corticolous species with anomalous peristomes are concentrated in *F.* subgen. *Polypodiopsis* sect. *Antennidens* and *F.* sect. *Neoamblyothallia* whereas most hydrophilous species with reduced peristomes belong to subgen. *Fissidens*. To answer such questions a different approach is needed, see for example Hedenäs (2012). I do hope, however, that the present paper will stimulate and facilitate future research.

MATERIAL, METHODS AND TERMINOLOGY

Descriptions are based on herbarium-material of corticolous African species and observations with a light microscope. For photography a Leica DM 2000 led microscope with Cannon Eos 6D camera were used. Stacking was done with Helicon Focus 7.6.1. Stacking, however, had to be used with moderation (at the most 2-3 photo's) because the OPL and IPL tend to get confused in the result.

Terminology and structure of the peristome

To describe anomalous peristomes it is necessary to understand the basic peristome of the Fissidentaceae. Fissidentaceae have an haplolepidous peristome (Edwards 1984) composed of a single row of 16 teeth and each tooth composed of two layers of cells, an outer layer (OPL) and an inner layer (IPL). During the formation of the tooth the adjoining parts of the walls of the OPL and IPL cells become partly thickened and the exterior parts disappear. Thus, the peristome-forming OPL and IPL cells become "roofless". On the exterior side each pair of teeth is built up by two columns of OPL cells, i.e. one column per tooth (Fig. 7F). On the interior side, each pair

is composed of three columns of IPL cells. The cells of the middle column are split and divided over the two teeth of the pair, thus each tooth is, on the inner side, formed by two columns, one of half cells and one of whole cells (Figs 7H; 16A1). The horizontal walls of both OPL and IPL cells are called trabeculae and the "floor" of the cell is the lamella. Peristome teeth of Fissidentaceae are, in the upper part, divided into two filaments. A tooth consists of a basal undivided part (Fig. 1B), a zone in which the bifurcation occurs (Fig. 1A, B) and two filaments. For additional illustrations see Edwards (1984), Bruggeman-Nannenga & Berendsen (1990) and Bruggeman-Nannenga (2021).

Peristomes of corticolous species often deviate from this basic type in being undivided, completely divided or irregularly divided. To the inexperienced eye it can be hard to decide whether a tooth is undivided or completely divided. However, when the teeth are undivided (or partly divided) there will be 16 teeth and when the teeth are completely divided there will be 32 teeth visible. The number of teeth is most easily counted in dry capsules at a low magnification (×10).

Even when the general structure is understood the study of peristomes can be difficult. The quality and availability of peristomes are often poor. Even when in perfect condition peristomes do not lie flat and in anomalous peristomes the OPL is frequently thin and more or less transparent. This transparency makes it hard to distinguish between the OPL or the IPL, even with careful focusing. In such cases recognizing the basic structure of the IPL is helpful (Fig. 7E-H). Taking photographs at different levels is also useful. For practical reasons emphasis in the descriptions below is on the OPL.

"Spiral" filaments. Brotherus (1901) distinguished between peristome teeth that are "spiralig verdickt" and peristome teeth that are "knotig verdickt". These terms were also used by Mueller (1973) and Ishihara & Iwatsuki (1992). However, as Mueller pointed out, this term is not correct. The filaments consist of two layers (IPL and OPL) each with a separate ornamentation of close oblique ridges (Fig. 4E, left below). At a superficial view the ornamentation of the two layers together produces the appearance of a spiral. In this paper I follow the tradition and call such filaments "spiral". Note that apart from this "spiral" ornamentation the filaments also become spirally twisted after the removal of the operculum.

"Hemispiral" is used when the ornamentation of close oblique ridges is restricted to one layer.

On term, mammillose is used for mammillose, unipapillose and all intergradations.

Illustrations

For each species a description and illustrations of the peristome are provided. Other sporophytic characters are briefly described, but usually not illustrated. Gametophytes are not elaborately described, but for each species a diagnosis and references to previous descriptions and illustrations (if any) are provided.

RESULTS

Genus *Fissidens* Hedw.
Subgenus *Polypodiopsis* (Müll.Hal.) Broth.
Section *Antennidens* (Müll.Hal.) Paris

Scariosus-type peristome (ancestral type)

Fissidens marthae Cardot
(Fig. 1)

Fissidens marthae is characterized by short, marginal to weakly intramarginal limbidia on the basal part of the vaginant laminae of all or most leaves, pluripapillose leaf cells, and costae ending 2-3 cells below the leaf apex. Corticolous, also saxicolous.

Peristome

Scariosus-type; filaments distinctly bend inwards when moistened, distally divided into two filaments, OPL of undivided part with close-packed, lamellar plates about as high as the trabeculae (Fig. 1A, B), ornamentation changing around the bifurcation, OPL cells around the bifurcation surrounded by a continuous wall formed by trabeculae and vertical walls (Fig. 1A, B) and torn into two halves beyond the splitting with the two halves bending outwards (Fig. 1A, B), filaments "spiral" (Fig. 1C); filaments strongly hygroscopic, teeth ± 300 µm long, 37.5-40 µm wide at base.

Sporophyte

Seta 1.9-2.2 mm long, smooth; capsule 0.6 × 0.25 mm, exothecial cell columns ± 32, the cells oblong to quadratic-oblong, collenchymatous; operculum 0.5-0.6 mm long; spores 8.0-12.5 × 7.0-9.5(-11.5) µm.

Description and illustration

Bruggeman-Nannenga (2006a: fig. 13F-J).

Remark

Figure 1 is included as an example of the ancestral *scariosus*-type peristome. More examples and an elaborate description of this type are found in Bruggeman-Nannenga (2021).

Anomalous peristomes

Fissidens ah-pengae Brugg.-Nann.
(Fig. 2)

Fissidens ah-pengae is characterized by wide, elimbate, oblong to oblong-lingulate leaves with rounded-obtuse tips, limbidia weak, restricted to the vaginant laminae of perichaetial leaves, smooth laminal cells, costae that end 2-6 cells below the leaf tips and undivided, densely papillose peristome teeth. It is the only corticolous subgen. *Polypodiopsis* species in Africa with smooth laminal cells. Corticolous on tree-ferns in lowland rainforest.

Peristome

Erect with slightly incurved distal parts (both dry and wet), ± undivided, (seemingly?) perforated (Fig. 2A, B), densely and

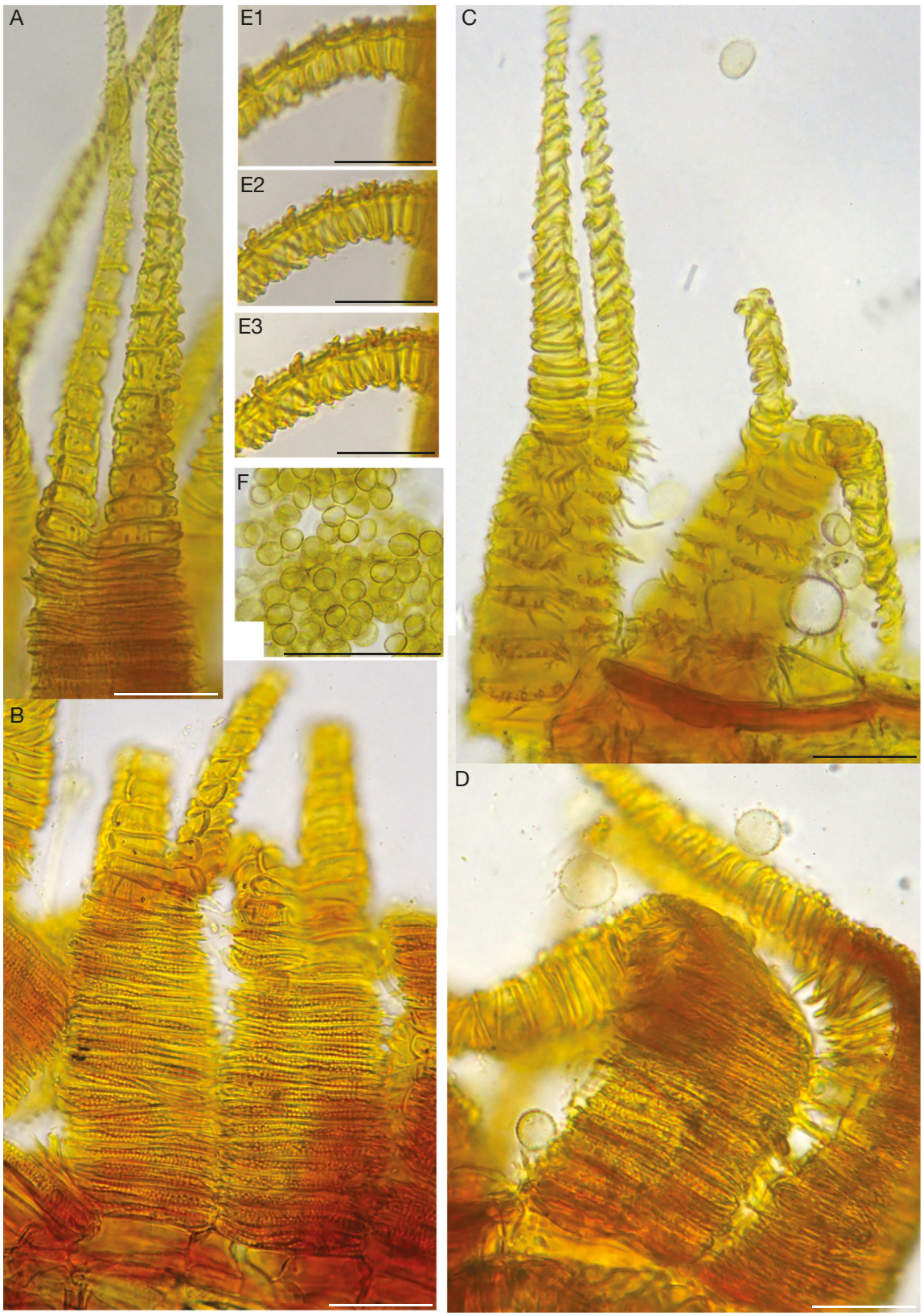

Fig. 1. — *Fissidens marthae* Cardot. **A**, OPL mid tooth, showing the bifurcation and filaments; **B,** OPL basal undivided part and bifurcation; **C,** IPL showing fimbriate trabeculae of the undivided part and high horizontal to oblique IPL ("spiral") ornamentation of the filaments; **D,** basal OPL of two teeth; **E1**-**3**, side-views of basal part of filament showing the low OPL and thicker IPL; **E1**, focus on the vertical walls of the OPL; **E3**, stack of E1 and 2; **F**, spores. **A**, **D**, **E** from Uganda, Mupanga Falls, *Porley U495A*, private herbarium Bruggeman-Nannenga; **B** from Tanzania, *Pócs 8633/M*, PC; **C**, **F** from Central African Republic, S. Ippy, Kéyorédé, *Tisserant s.n.*, PC. Scale bars: A-E, 20 µm; F, 50 µm.

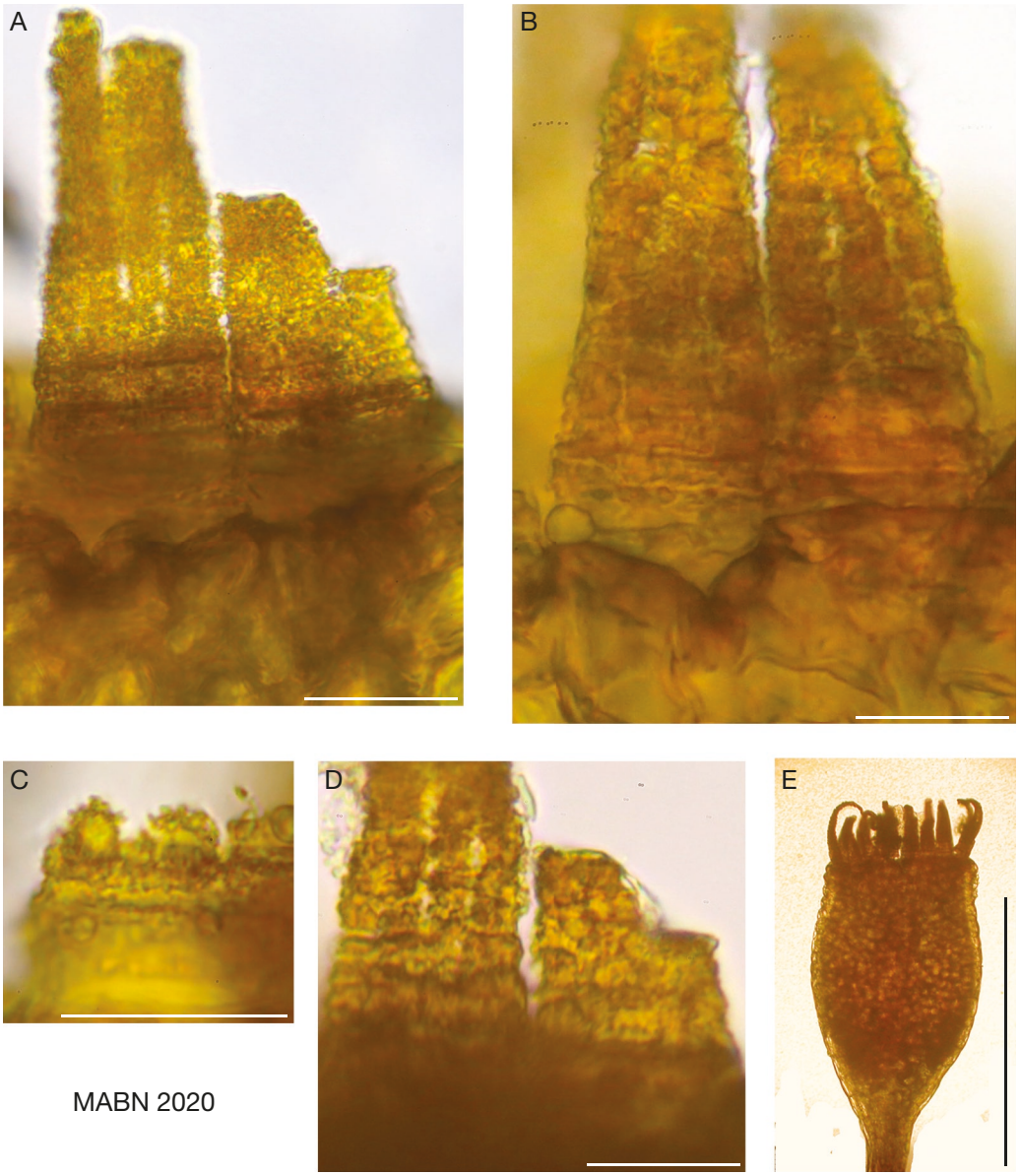

Fig. 2. — *Fissidens ah-pengae* Brugg.-Nann. **A**, OPL with focus on the thin trabeculae; **B**, OPL focus on the through-shining 3-4 irregular columns IPL cells; **C**, two IPL trabeculae with a papillose margin; **D**, IPL; **E**, moist capsule with ± erect, gently incurved teeth. All from holotype, La Réunion, Commune de Saint-Philippe, *Ah-Peng & Bardat s.n.*, private herbarium Bruggeman-Nannenga. Scale bars: A-D, 20 µm; E, 0.4 mm.

coarsely papillose, ± 100 µm long, 26-30 mm wide at base; distal parts breaking off easily.

Ornamentation
OPL trabeculae thin, most distinct in basal cells (Fig. 2A); mid and distal part coarsely papillose interspersed with "perforations"; IPL trabeculae of basal IPL cells with a papillose border (Fig. 2C), IPL in mid and upper part with irregularly thickened, papillose plaques forming a pattern of 3(-4) irregular columns that disturb the normal IPL structure of two columns (Fig. 2B, D).

Sporophyte
Seta ± 1 mm long, smooth; capsule cylindrical, 0.4 × 0.3 mm, exothecial cell columns ± 32, the cells quadratic-oblong to oblong; operculum not observed; spores ± 15 µm in diam., smooth.

Description and illustration
Bruggeman-Nannenga (2009: fig. 1); Bruggeman-Nannenga & Arts (2010: fig. 18).

Remarks
In this species the OPL is difficult to distinguish from the through-shining IPL. It is not clear whether the perforations are thin areas or true perforations. The peristome of *F. ah-pengae* resembles that of *F. punctulatus* Sande Lac. in being densely and coarsely papillose and seemingly perforated.

Fissidens arboricola Brugg.-Nann.
(Fig. 3)

Fissidens arboricola is characterized by mammillose laminal cells, limbidia restricted to the upper leaves of perichaetial stems, costa evanescent (excurrent in some perichaetial leaves), spores large, 23.5-32.5 µm diam., peristomes anomalous, deeply to completely divided, with "spiral" filaments. Grows in mats and between mosses and liverworts on the bark of small trees and twigs.

Peristome
When moistened the teeth more or less straighten, teeth deeply to completely divided, undivided part 0-3 cells tall, filaments "spiral", teeth 140-190 µm long and tooth base 28-40 µm wide.

Ornamentation
OPL of both the undivided part and the bifurcation with distinct smooth trabeculae, lamellae smooth or ± smooth (difficult to ascertain because of the through shining IPL; in completely divided teeth lamellae with delicate oblique ornamentation), in mid and distal parts ornamentation of high oblique ridges; IPL trabeculae well developed, lamellae of undivided part with close, horizontal to oblique ridges "hemispiral", filaments "spiral".

Sporophyte
Seta ± 1 mm long, almost smooth; capsule narrowly cylindrical, 0.8-1.1 × 0.3 mm, exothecial cells columns ± 32, cells oblong with thickened vertical walls; operculum rostrate, 0.25 mm long; spores large, 23.5-32.5 diam., papillose.

Description and illustration
Bruggeman-Nannenga (in press: 38; fig. 1).

Fissidens aristifer Brugg.-Nann.
(Fig. 4)

Fissidens aristifer is characterized by the apices of the perichaetial leaves being asymmetrical with long excurrent costae, mammillose laminal cells, limbidia restricted to the vaginant laminae of distal leaves of perichaetial stems, numerous budlike, axillary perigonia just below the terminal perigonium, archegonia terminal on branches as well as on main stems, short setae, narrow, cylindrical thecae and anomalous, peristomes with teeth that are (almost) completely divided and have "spiral" filaments. Growing between mosses and liverworts on bark of small tree.

Peristome
This species has deeply divided peristome teeth, undivided part ± 4 cells tall on OPL side with distinct trabeculae and smooth or almost smooth lamellae, filaments "spiral". The teeth are 100-240 µm long and the tooth base is 33-41 µm wide. When moistened the teeth promptly straighten.

Ornamentation
In the OPL three zones can be distinguished: an undivided part with smooth trabeculae and lamellae, a bifurcation with low smooth trabeculae and variously ornamented lamellae, papillose (Fig. 4F) to vertically striate (Fig. 4D); in the IPL two zones are distinguishable (Fig. 4B), the undivided part with high, papillose trabeculae and the filaments; filaments terete, "spiral" (Fig. 4E).

Sporophyte
Seta 0.9-1.5 mm, ± smooth; capsule cylindrical, 0.6-0.9 × 0.25-0.45 with exothecial cell columns ± 32, the cells oblong with thickened vertical walls; operculum bluntly rostrate, 0.35 mm, spores 18.5-22.5 µm long (in type), 21.0-29.5 µm (in *Pócs 6991/F*), papillose.

Description and illustration
Bruggeman-Nannenga (2009: fig. 2); Bruggeman-Nannenga & Arts (2010: fig. 20).

Remark
Peristomes of this species vary in ornamentation. The above description is from the type specimen.

Fissidens cyathaeicola Brugg.-Nann.
(Fig. 5)

This relatively large species, 6.0 × 0.5 mm, is characterized by ½ limbate vaginant laminae, pluripapillose laminal cells and erect, narrow, undivided or irregularly divided peristomes with papillose filaments. In mats or scattered on bark of tree ferns.

Peristome
Slightly curved inwards when wet, stiff, undivided or irregularly divided. Teeth with short, up to 5 cells high, undivided part and a papillose distal part 150 µm long, tooth base 30-32.5 µm wide, rudimentary second filament (Fig. 5C) occasionally present.

Ornamentation
OPL short, ± 5 cells tall, undivided basal part with distinct, smooth trabeculae and ± smooth lamellae; the first cell above the bifurcation with distinct trabeculae and vertical walls and a sparse lamellar ornamentation; more distal cells densely and lowly papillose; IPL papillose throughout the teeth, IPL cells thicker than the thin, transparent OPL cells (Fig. 5C); filaments papillose.

Sporophyte
Seta 1.2-1.5 mm long, smooth; capsule 0.5 × 0.2-0.3 mm with exothecial cell columns 26-32, the cells thin-walled, oblong; operculum ± 0.2 mm long; spores 9.0-13.5 µm diam., papillose.

Description and illustration
Bruggeman-Nannenga & Arts (2010: fig. 21).

Fissidens diaphanodontus (P. de la Varde) Bizot
(Fig. 6)

Fissidens diaphanodontus is characterized by oblong-lanceolate leaves with broadly acute to rounded, obtuse often apiculate apex, conico-mammillose laminal cells, limbidia limited to the upper leaves of

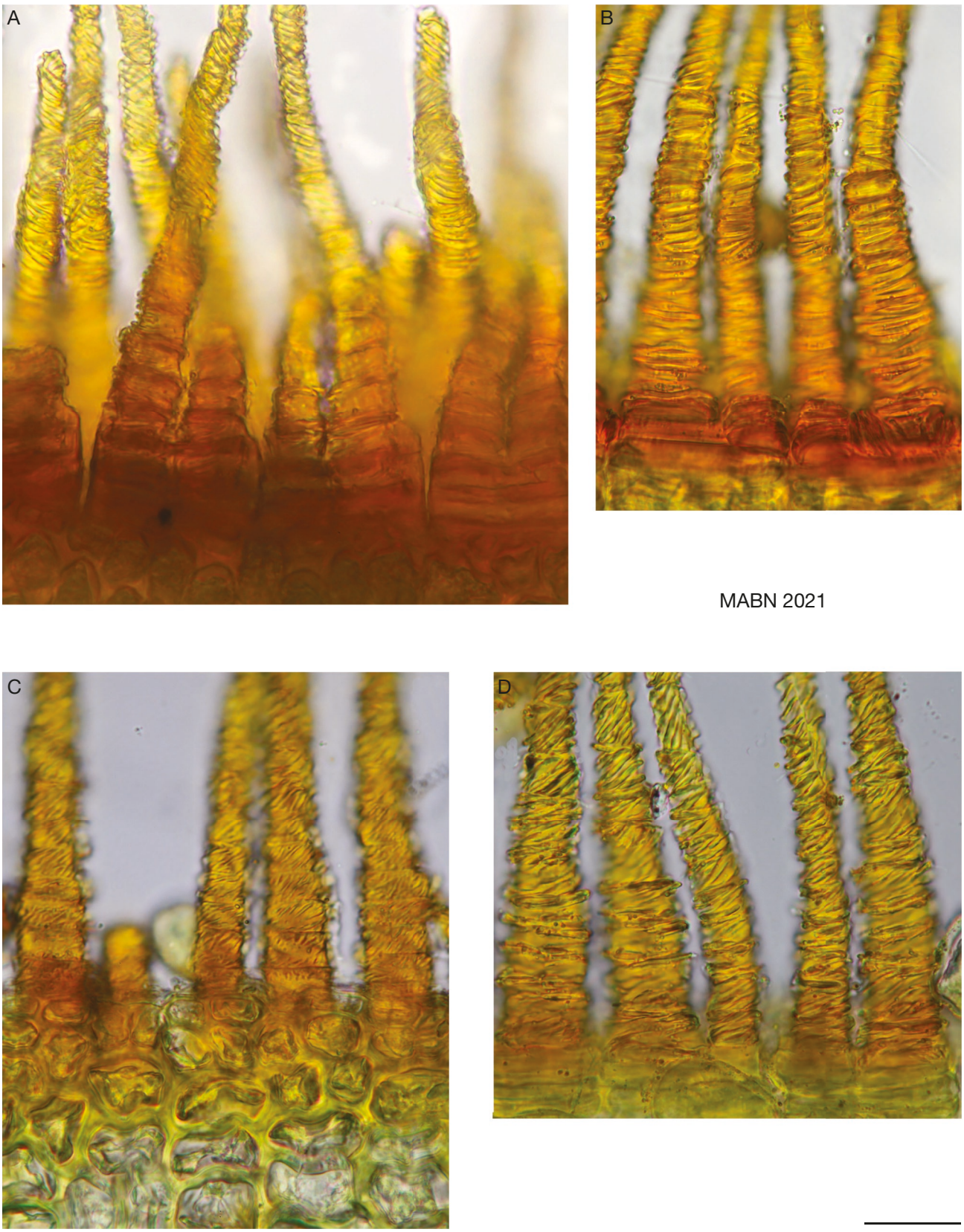

FIG. 3. — *Fissidens arboricola* Brugg.-Nann. **A**, **B**, deeply divided peristome teeth; **C**, **D**, completely divided peristome teeth. **A**, OPL, in the background spiral filaments; **B**, IPL of two teeth with high, close horizontal to oblique ridges ("spiral"); **C**, OPL, the trabeculae are recognizable as thin lines, lamellar ornamentation of close oblique ridges; **D**, IPL basal and mid part with high, close oblique ridges. **A**, **B** from Madagascar, Toamasina, Analamazotra Forest Station, *Brinda 12240* (type MO, L); **C**, **D** from Madagascar, Tulear, Forêt d'Analamaro, *ALR-237*, private herbarium Bruggeman-Nannenga. Scale bar: 20 µm.

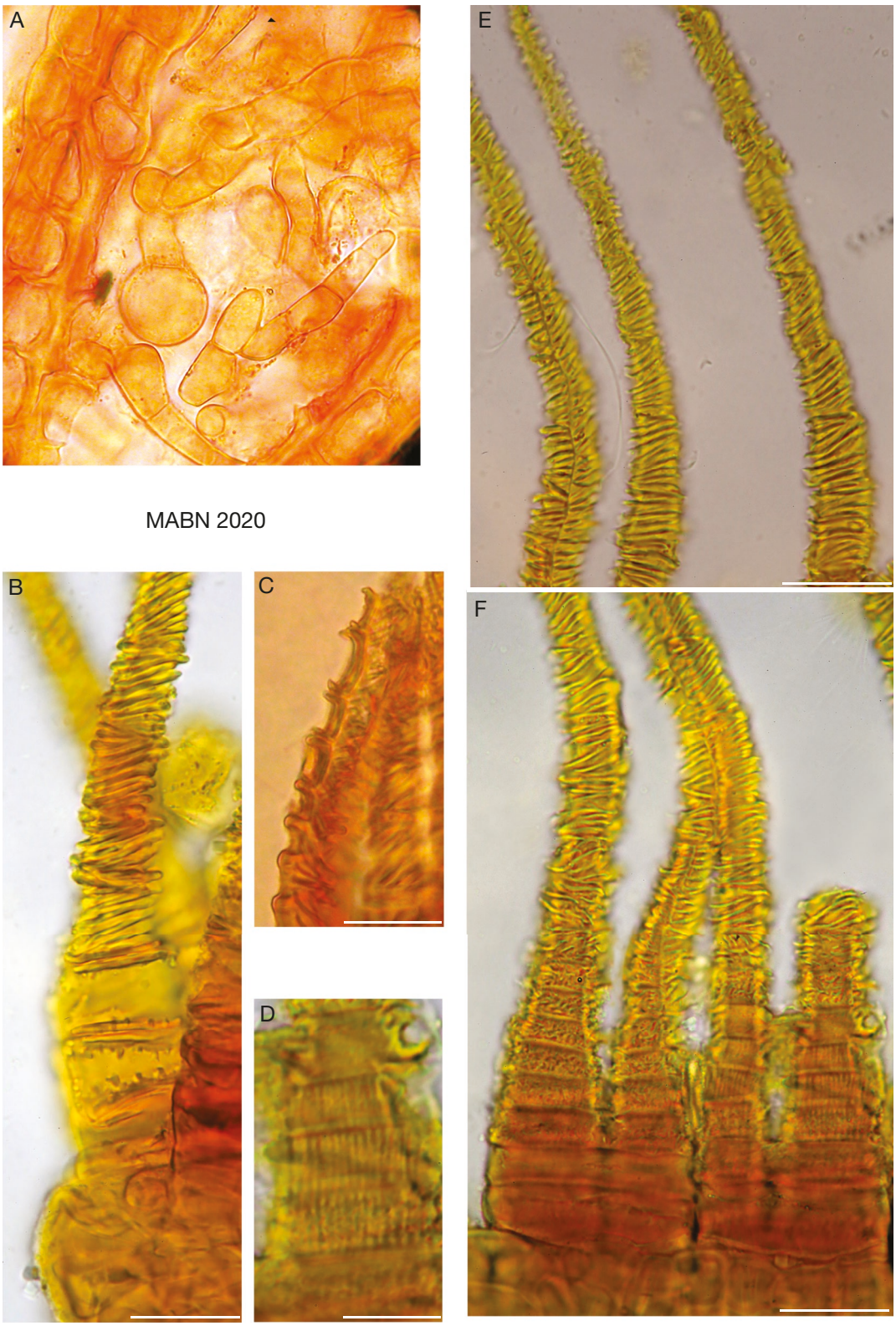

Fig. 4. — Peristome of *Fissidens aristifer* Brugg.-Nann. **A**, spores germinating in capsule; **B**, IPl of undivided part showing papillose trabeculae and ± smooth lamellae; more distally the high, oblique ornamentation of the filament is seen; **C**, side view showing double protruding trabeculae (on the left) and vertical walls of the OPL; **D**, detail of F showing delicate vertical lamellar ornamentation of the OPL; **E**, filaments, in the left filament the border between IPl and OPl clearly visible; **F**, OPL of two teeth. **A**, **C** from La Réunion, Jacques Payet, Sentier du Volcan, *Arts RÉU 153/30*, BR, private herbarium Bruggeman-Nannenga; **B**, **D**-**F** from type: Madagascar, Ambatofitorahana, *Onraedt 70.M.0453,*BR: BR-BRY 238507 – 81. Scale bars: B, E, F, 20 µm; C, D, 10 µm.

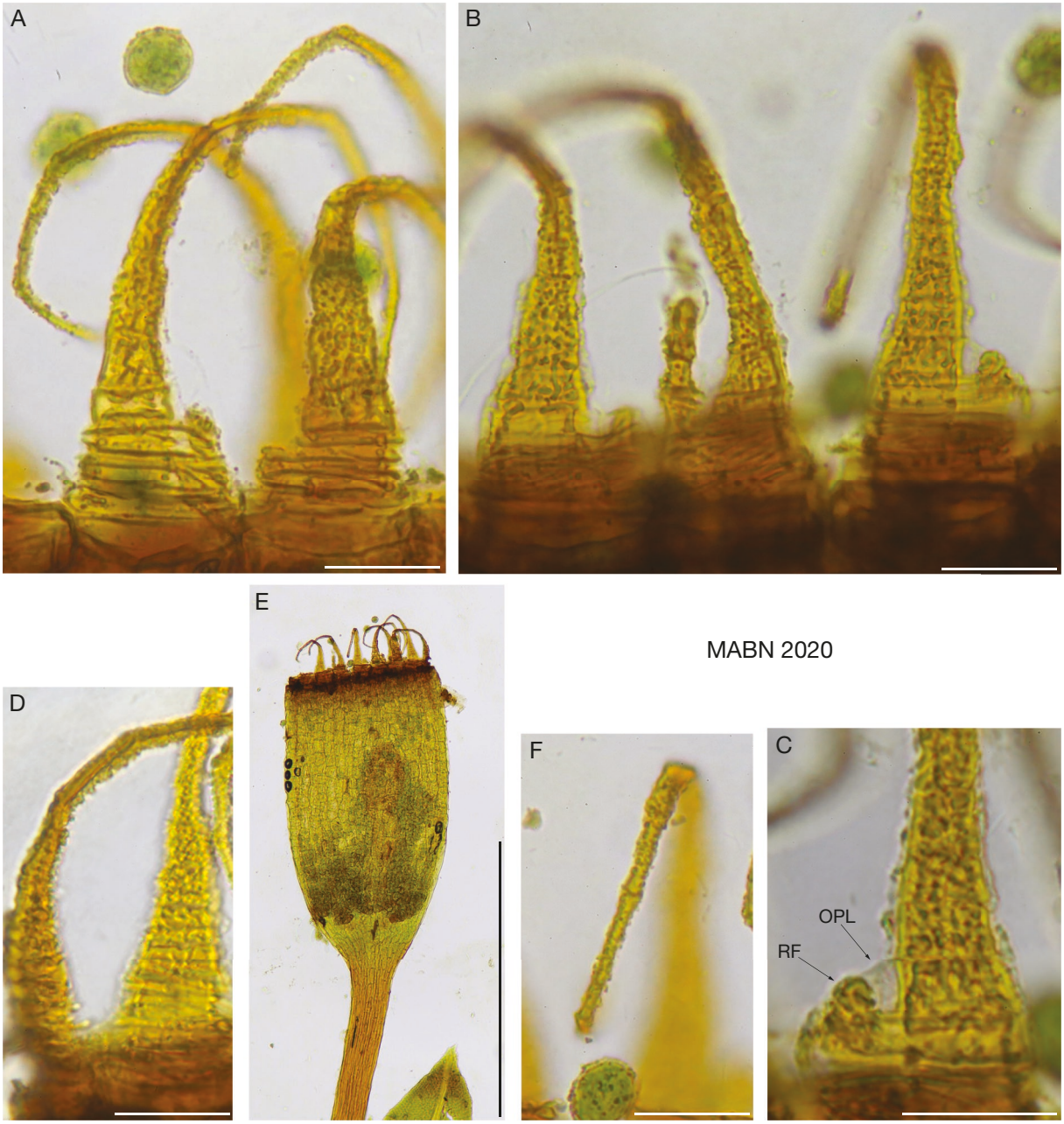

FIG. 5. — *Fissidens cyathaeicola* Brugg.-Nann. **A**, OPL of two teeth. The left tooth with rudimentary filament on the right; **B**, IPL of three teeth, all with rudimentary second filament; **C**, IPL of basal part of tooth with rudimentary filament (RF). Note the transparent OPL that is wider and thinner than the IPL; **D**, mid part of tooth in side view, on the left IPL of second tooth; **E**, capsule; **F**, OPL of distal filament. All from holotype, La Réunion, Forêt de Bélouve, *Bruggeman-Nannenga 11044*, L, REU. Scale bars: A-D, F, 20 µm; E, 0.5 mm.

perichaetial stems and short costae ending 2-11 cells below the apex. Growing between mosses and liverworts on bark of trees.

Peristome

Straightening when moistened, erect to slightly curved inwards, stiff, undivided, up to 100 µm long. This characteristic peristome is easily recognized by its unique fenestrate appearance.

Ornamentation

OPL with basal five or six cells fenestrate with strongly papillose trabeculae and vertical walls surrounding the smooth lamellae, more distally the trabeculae and vertical walls become indistinct and the lamellae densely papillose or with indistinct oblique ridges; basal six to nine IPL cells like the basal OPL cells but more coarsely papillose, distal part densely papillose. OPL and IPL thin, IPL slightly thinner than the OPL (Fig. 6F).

Sporophyte

Seta 1.4 mm long, ± smooth; capsule cylindrical, 0.5-0.55 × 0.2 mm with exothecial cell columns ± 32, the cells oblong with thickened vertical walls, operculum not observed, spores 13.5-17.5 × 12.0-16.0 µm, papillose.

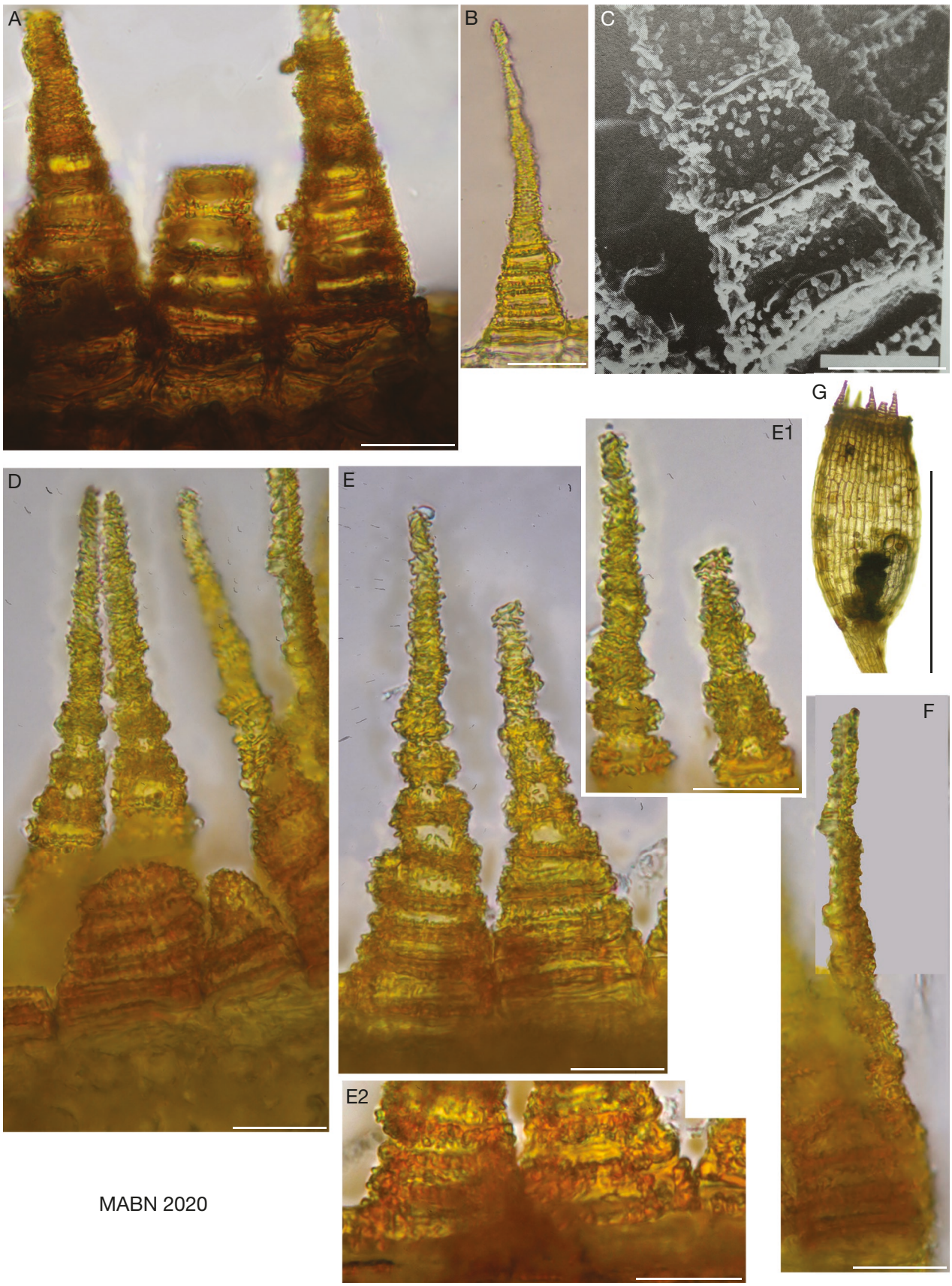

FIG. 6. — *Fissidens diaphanodontus* (P.de la Varde) Bizot. **A**-**C**, OPL; **C**, SEM photograph; **D**, **E**, IPL; **D**, with OPL in foreground; **E1**, distal filaments; **E2**, basal cells; **F**, side view of tooth; **G**, moist capsule with erect peristome teeth. **A**, **B**, **G** from Guinea, Nzérékoré Region, Macenta Prefecture, *Lisowski 100*, private herbarium Bruggeman-Nannenga, KRAM; **C** from Inoue, Bryoph. Sel. Exsic. 580, L; **D**-**F** from Tanzania, *Pócs 6387/Q*, PC; **C** previously published in Bruggeman-Nannenga & Berendsen1990. Scale bars: A, D-F, 20 µm; B, 25 µm; C, 10 µm; E1-2, 20 µm; G, 0.5 mm.

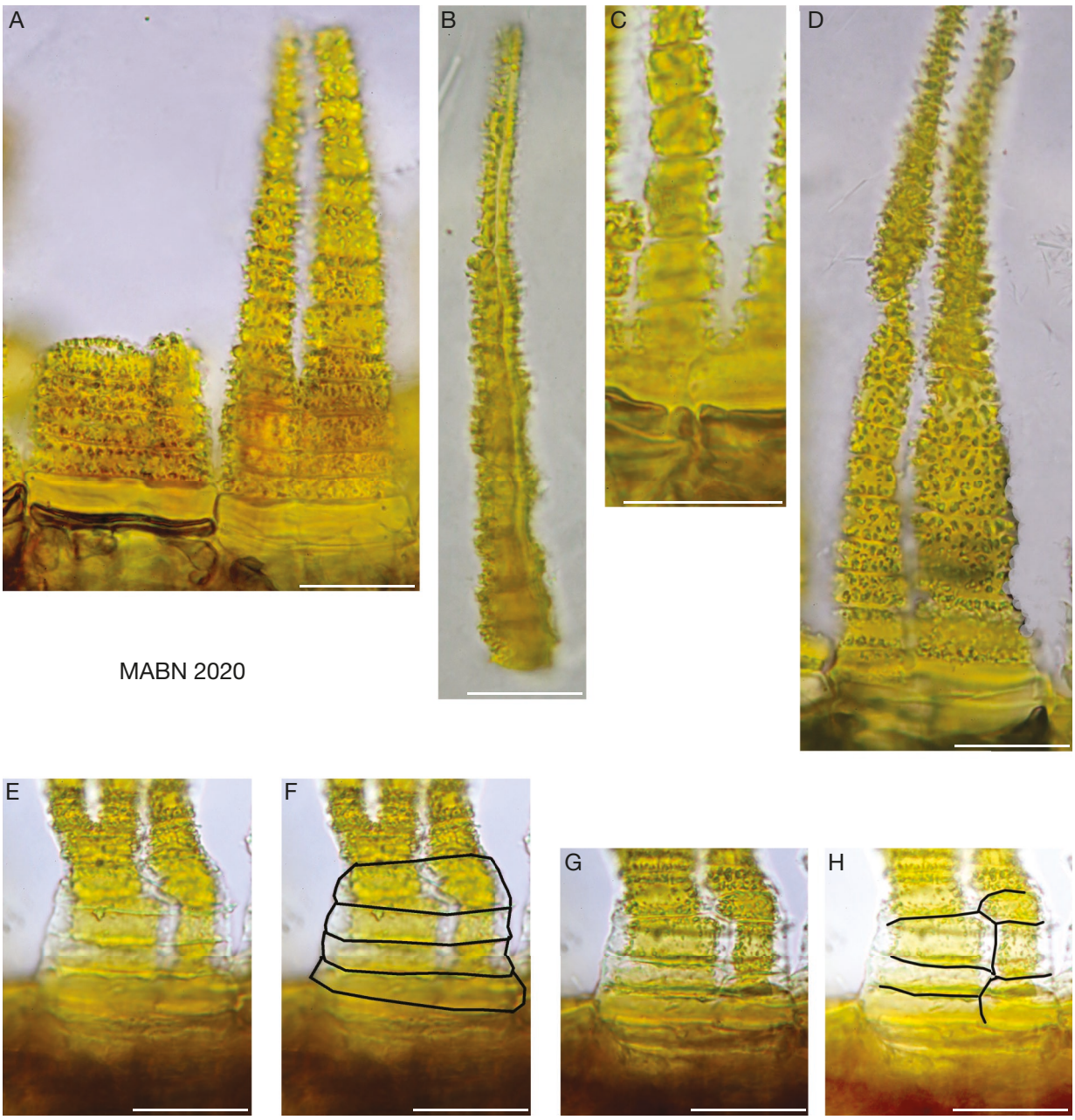

FIG. 7. — *Fissidens gardneri* Mitt. **A**, OPL of undivided part of two teeth (left one broken off); **B**, side view of tooth; **C**, IPL lamellae with focus below the papillose surface to show the incrassate platelets; **D**, as C with focus on the papillose outer surface; **E**-**H**, same tooth at different levels; **E**, undivided part and bifurcation, or rather trifurcation with focus on the transparent OPL, the underlaying IPL is clearly visible; **F**, photo E with OPL cells outlined to show the single column of OPL cells; **G**, focus on IPL; **H**, photo G with IPL cells outlined to show the two columns with the zigzag border line. **A**-**D** from Tanzania, WSW of Morogoro town, *Pócs 87041/R*, EGR, private herbarium Bruggeman-Nannenga; **E**-**H** from Madagascar, Fianarantsoa, *Magill* & *Crosby 12919*, MO. Scale bars: 20 µm.

Description and illustration
Bruggeman-Nannenga & Berendsen (1990: fig. 5b); Potier de la Varde (1951: fig. 2).

Fissidens gardneri Mitt.
(Fig. 7)

This tiny species is characterized by open to almost open vaginant laminae, pluripapillose cells, the mostly obtuse leaf apex, costae ending far below the leaf apex and in the upper part often covered by laminal cells, limbidia restricted to the vaginant laminae of the upper leaves of perichaetial plants, undivided to irregularly divided, straight papillose peristome teeth and large spores. Scattered on bark of trees often not mixed with other mosses.

Peristome
± straight when dry, ± straight when wet, stiff, divided, irregularly divided or undivided, basal undivided part 3-4 cells tall, teeth 100-145 µm long, tooth base 25.5-32 µm wide.

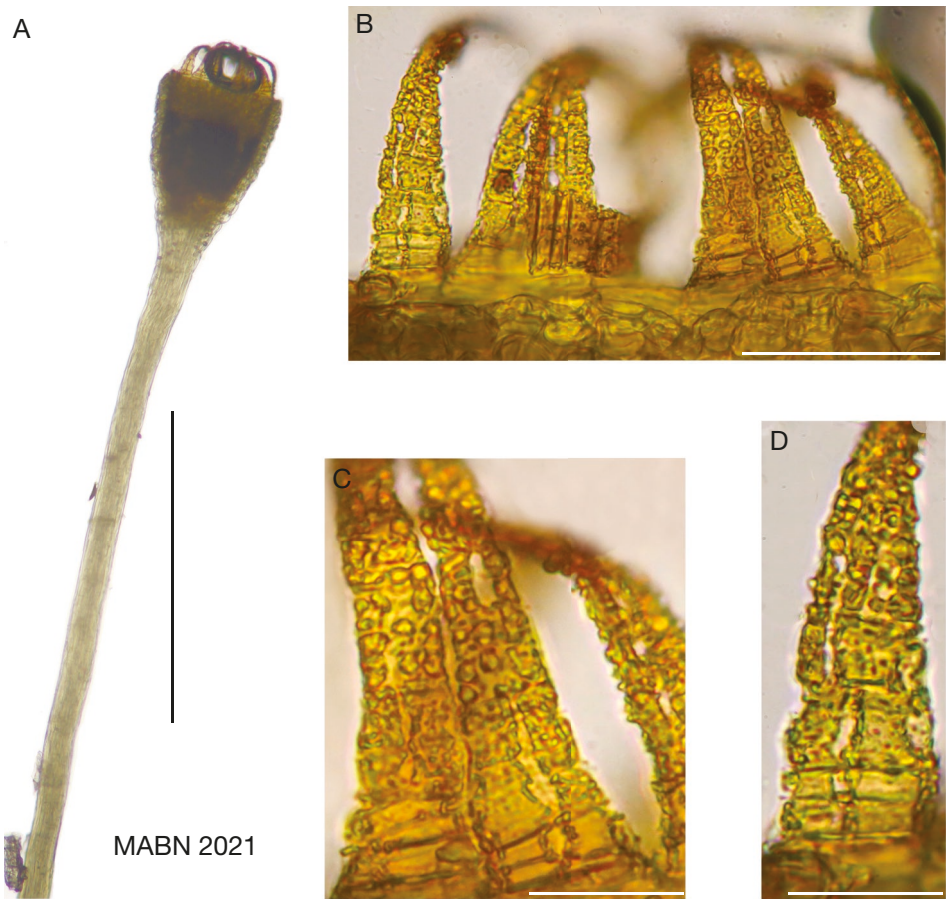

FIG. 8. — *Fissidens granulidens* Brugg.-Nann. **A**, seta with capsule (moist); **B-D**, impressions of the peristome. All from holotype, Madagascar, forêt primitive de Manjkatompo, *Heim s.n.*, PC0773629A. Scale bars: A, 0.5 mm; B, 50 µm; C, D, 20 µm.

Ornamentation
OPL basal 2-4 cells with high, smooth, thin trabeculae and smooth to papillose lamellae, thickness and transparency of basal OPL variable (compare Fig. 7A, E); IPL basal 3-4 cells with high, papillose trabeculae and smooth (or papillose?) lamellae; IPL lamellae incrassate (Fig. 7C) with densely papillose surface (Fig. 7D); mid and distal part of both OPL and IPL papillose.

Sporophyte
Seta 1-1.5 mm long, smooth; capsule cylindrical, 0.45-0.55 × 0.25-0.3 mm, exothecial cell columns ± 32, of the cells oblong exothecial cells; operculum 0.25 mm long; spores subglobose to ellipsoid, large, 20-37 µm, thick-walled, coarsely papillose, occasionally germinating in the capsule.

Description and illustration
Pursell (2007: fig. 76L).

Fissidens granulidens Brugg.-Nann.
(Fig. 8)

This tiny corticolous species is best characterized by its granulose, undivided peristome and laminal cells with ± 2 large papillae with a blunt, rounded apex that with oil-immersion looks rugose. Growing on bark.

Peristome
Slightly incurved when moistened, undivided, thin with granulose ornamentation; teeth ± 50 µm long, tooth base 17-20 µm wide. Only one capsule known. Peristome distinctive, due to the transparency it is impossible to distinguish between OPL and IPL. The joint appearance of OPL and IPL is that of granulose teeth with partly thickened lamellae.

Sporophyte
Seta 1 mm long, smooth, basal part somewhat rugose; capsule cylindrical 0.3 × 0.2 mm with exothecial cell columns ± 22, the cells oblong, thin-walled; operculum not seen; spores subglobose, 19-21.5 × 17-19 µm, papillose.

Description and illustration
Bruggeman-Nannenga (in press: 40; fig. 2).

Fissidens inclusus Bizot & Dury ex Pócs
(Fig. 9)

Fissidens inclusus is characterized by short, 0.7-0.8 mm long, setae, vaginant laminae with revolute margins, mammillose cells, limbidia restricted to the upper leaves of perichaetial stems and divided peristomes. It is closely related to *F. pocsii* Bizot & Dury ex Pócs

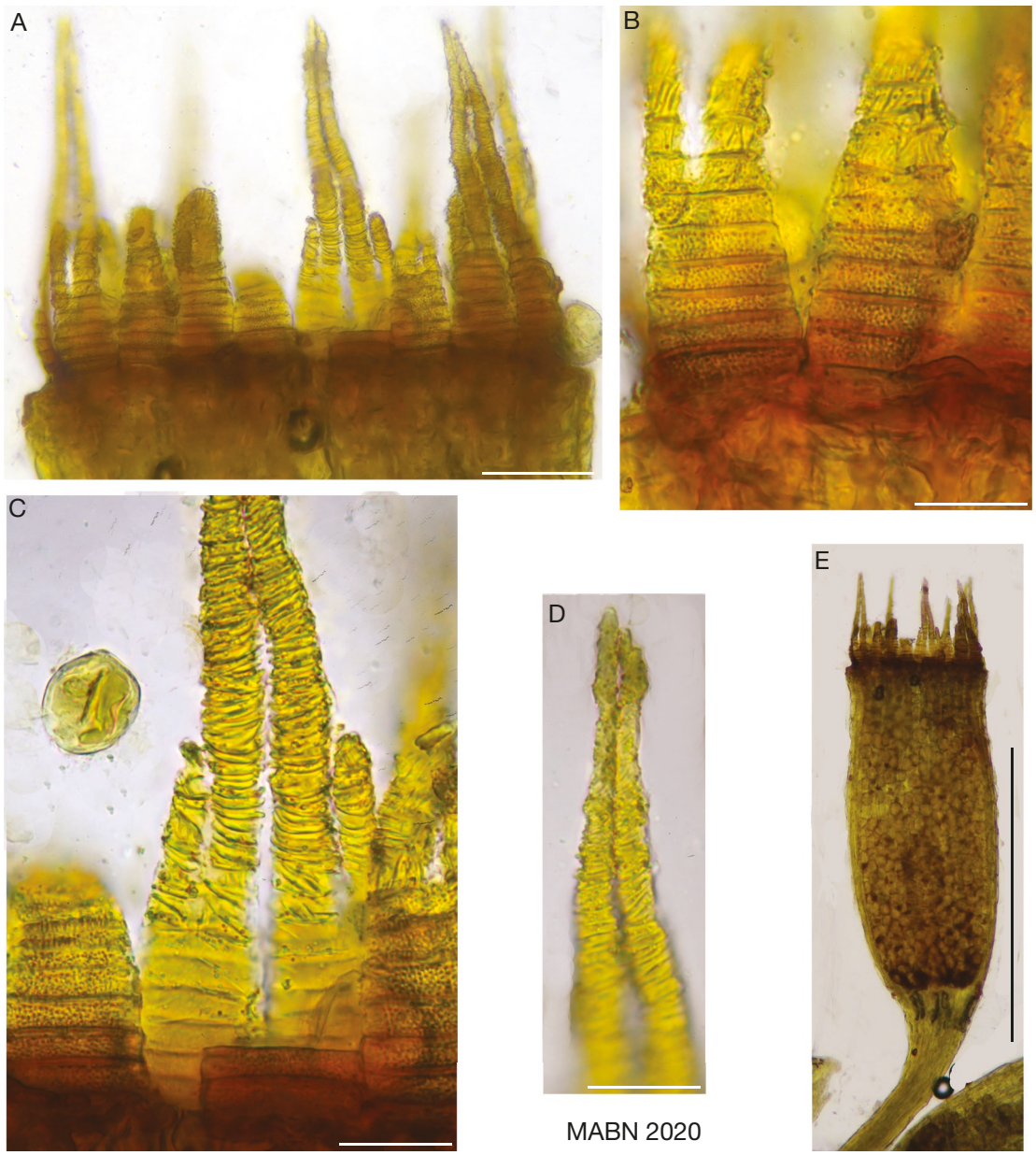

Fig. 9. — *Fissidens inclusus* Bizot & Dury ex Pócs. **A**, capsule mouth with peristome. Four teeth on the left and three on the right seen from the OPL-side, in the mid IPL of pair of teeth; **B**, OPL of undivided part and bifurcation; **C**, IPL basal part and basal filaments plus spore; **D**, IPL distal filaments; **E**, capsule (moist) with straight erect teeth. All from holotype, Tanzania, Nguru Mts, on the ridge S of Kwamanga Village above Mhonda mission nr Turiani, *Pócs & Mabberley 6398/A*, EGR. Scale bars: A, 50 µm; B-D, 20 µm; E, 0.5 mm.

sensu lato. For differences see under that species. Growing on twigs in loose pure mat.

Peristome

Erect to curved inwards when wet, divided, often broken off; teeth 122-166 µm long, at the base 20-29 µm wide.

Ornamentation

OPL undivided part ± 8 cells tall, with high, thin, smooth trabeculae and finely papillose lamellae; around bifurcation trabeculae distinct and lamellae with sparse ornamentation of oblique ridges; IPL basal 4 cells with high trabeculae and ± smooth (hard to see) lamellae; bifurcation with high oblique ridges; both OPL and IPL of filaments with dense ornamentation of oblique ridges ("spiral"). This peristome resembles a weak *bryoides*-type peristome with short filaments. The *bryoides*-type peristome is diagnostic for subgenus *Fissidens*. *Fissidens inclusus* however, has a subgen. *Polypodiopsis* gametophyte. This problem is considered later in the discussion.

Sporophyte

Seta 0.7-0.8 mm long, smooth to ± rough; capsule cylindrical to narrowly cylindrical, 0.6-0.7 × 0.3-0.35 mm, exothecial

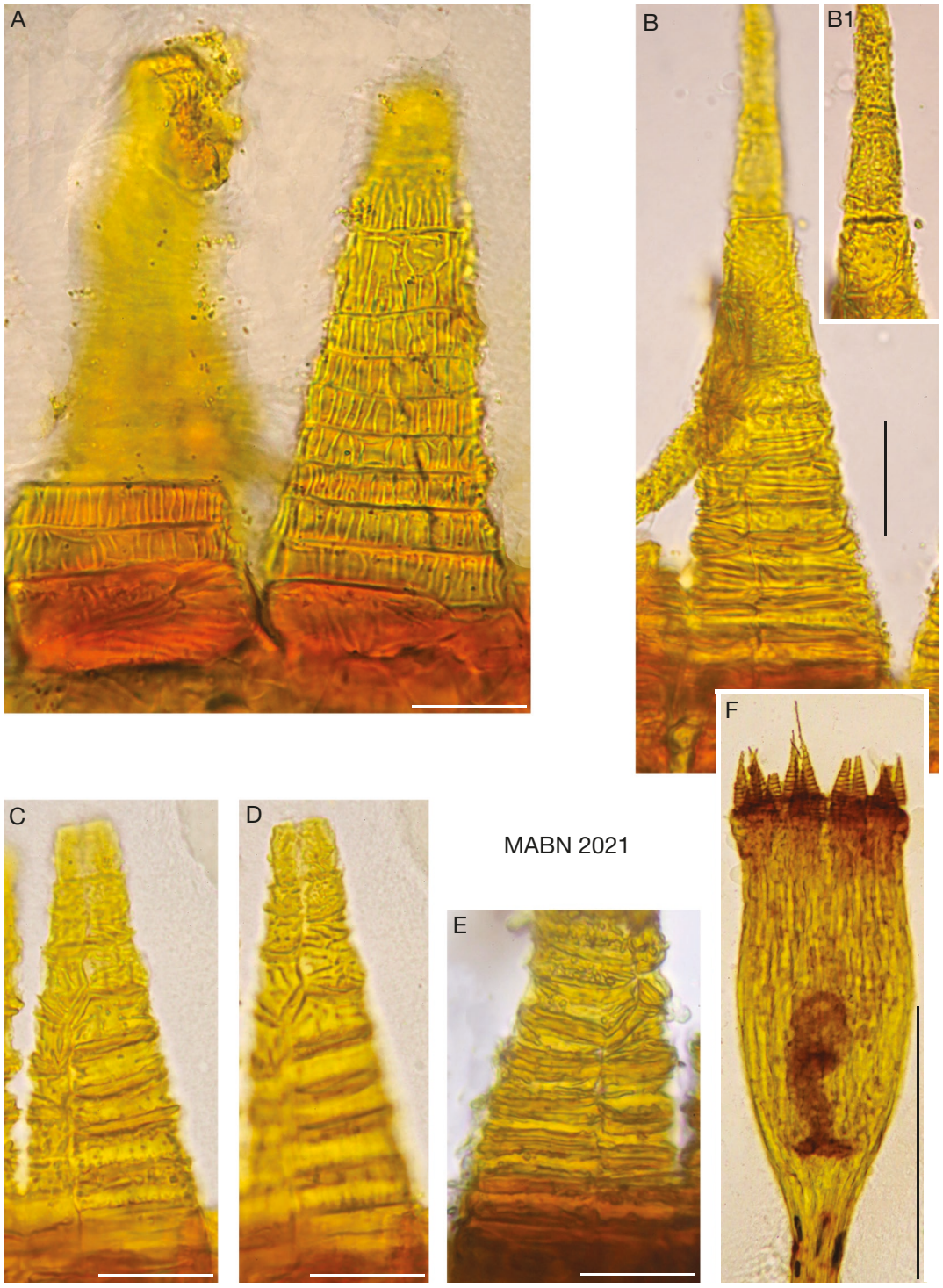

FIG. 10. — *Fissidens jonesii* Bizot ex Pócs. **A**, OPL of two teeth (left one broken off) showing the characteristic trellis-like ornamentation; **B**, IPL of tooth; **B1**, detail of distal tooth; **C**, IPL basal part of tooth; **D**, same tooth as C with focus on the distal ornamentation; **E**, IPL basal part; **F**, moist capsule with erect peristome teeth. **A**, **B** from Tanzania, Uluguru Mountains, E slope of Bondwa, *Pócs et al*. *6260/A*, EGR; **C**-**E** from Tanzania, *Pócs 8616/F*, EGR; **F** from Tanzania, *Pócs 6260/B*, EGR. Scale bars: A-E, 20 µm; F, 0.5 mm.

cell columns ± 32, the cells oblong, operculum not observed, spores (17.5-)19-25(-28) × 15.5-23 µm (almost smooth).

Description
Bizot (1974: 132).

Fissidens jonesii Bizot ex Pócs
(Fig. 10)

This species is characterized by mammillose cells, well developed limbidia restricted to the upper leaves of perichaetial stems, bud-like

axillary perigonia and by its characteristic thin peristomes with a trellis-like ornamentation. Growing scattered on tree ferns.

Peristome
Distal ends slightly curved inwards when moist, undivided, thin, often broken off, teeth ± 130 µm long (hard to measure), tooth base 27-35 µm wide.

Ornamentation
OPL thin, basal 9 cells with thin, smooth, trabeculae and lamellae with vertical lamellar ridges (Fig. 10A); more distally the lamellae become papillose; IPL basal 8 cells with thick, double, somewhat papillose trabeculae and smooth to sparsely papillose lamellae; towards the apex the teeth gradually becoming papillose (Fig. 10B1). Filaments thin, on both OPL and IPL papillose.

Sporophyte
Seta 0.65-1.8 mm long, smooth to rough, not papillose; capsule cylindrical to narrowly cylindrical, 0.7-0.8 × 0.25-0.35 mm, with exothecial cell columns ± 32, the cells oblong with thick vertical walls, operculum not observed, spores variable in size, 15-26.5 µm, papillose.

Description and illustration
Bizot (1974: 133); Bruggeman-Nannenga (in press: 46; fig. 6).

Fissidens lagenarius Mitt.
(Fig. 11)

Pantropical, mammillose species with limbidia restricted to the upper leaves of perichaetial stems and ± divided peristomes with a characteristic ornamentation. OPL lamellae in mid teeth with spaced, irregular oblique to vertical ridges in the mid part of the teeth (Fig. 11A, B). Rare in Africa, known from two collections, both with rather poor peristomes. Part of the above description is therefore based on Neotropical specimens.

Peristome
± erect when wet, stiff, undivided in the two African specimens (undivided or imperfectly and irregularly divided according Pursell (2007) in his neotropical monograph, teeth 66-200 µm long, tooth base 22-33 µm wide, distal parts papillose, often broken off or rudimentary.

Ornamentation
OPL basal ± 3 cells with high, smooth trabeculae and thin lamellae that are wider than the IPL-lamellae, in distal direction the trabeculae gradually become indistinguishable, lamellae from about the 4-th cell onwards with an irregular pattern of spaced, vertical to diagonal ridges (Fig. 11A, B), near the apex papillose; IPL in the basal part over a short distance with two columns (Fig. 11D, F), sometimes with a single column throughout (Fig. 11C); the ± 5 basal-most cells with high, papillose trabeculae and ± smooth lamellae, more distal lamellae with close, oblique to horizontal close ridges; filaments papillose on both sides, often broken off; IPL thicker than the OPL (Fig. 11G).

Sporophyte
Seta 0.9-1.5 mm, smooth; capsule narrow and long, 0.45-0.6 × 0.2-0.25 mm, exothecial cell columns ± 32, the cells oblong, operculum not observed, spores 17.5-20.5 × 16-18.0 µm, finely papillose.

A rather similar peristome is found in the Brazilian *Fissidens scindulosus* Brugg.-Nann. This species differs from *F. lagenarius* by scindulose cells with 1-3 scindulae. Scattered or in loose mats, hardly mixed.

Description and illustration
Buck (2003: fig. 10G-I); Pursell (2007: fig. 94); Bruggeman-Nannenga (2011: fig. 26C, E, G, I, J).

Fissidens macroglossus (Broth.) Brugg.-Nann.
(Fig. 12)

Fissidens macroglossus is characterized by wide, oblong to lingulate leaves, limbidia restricted to upper leaves of female stems reaching to half the length of the vaginant laminae, costae ending 9-21 cells below the apex, distal parts of the costae over a short or long distance covered by chlorophyllose cells, vaginant laminae slightly open, pluripapillose cells, peristomes undivided or irregularly divided, lamellae of undivided basal OP cells smooth, distal tooth parts densely papillose. On bark in a pure mats.

DISTRIBUTION. — West African endemic.

Peristome
Slightly curved inwards when moist, teeth stiff, undivided to deeply divided, 150-165 µm long, tooth base 36-40 µm wide, distal parts papillose.

Ornamentation
Basal three OPL cells undivided with smooth trabeculae and smooth lamellae, more distal lamellae papillose (“hairy”) (Fig. 12B, C); IPL basal trabeculae with papillose edges (Fig. 12F), basal lamellae smooth? (hard to observe), in distal direction the trabeculae become obsolete, lamellae of mid and distal part often incrassate, densely papillose.

Sporophyte
Seta 1.2-1.5 mm long, ± smooth; capsule cylindrical, 0.6-0.8 × 0.25-0.3 mm (not conspicuously narrow), with exothecial cell columns ± 30-38, the cells oblong; operculum 0.25 mm long, spores subglobose, 18-24 µm, papillose.

Description
Brotherus (1931: 27).

Fissidens papillisetus Brugg.-Nann.
(Fig. 13)

Fissidens papillisetus is characterized by lanceolate, acute to slightly acute-acuminate leaves, margins of vaginant laminae plane, laminal cells mammillose, limbidia as a rule well developed, intramarginal, setae and calyptrae strongly papillose and peristomes with undivided

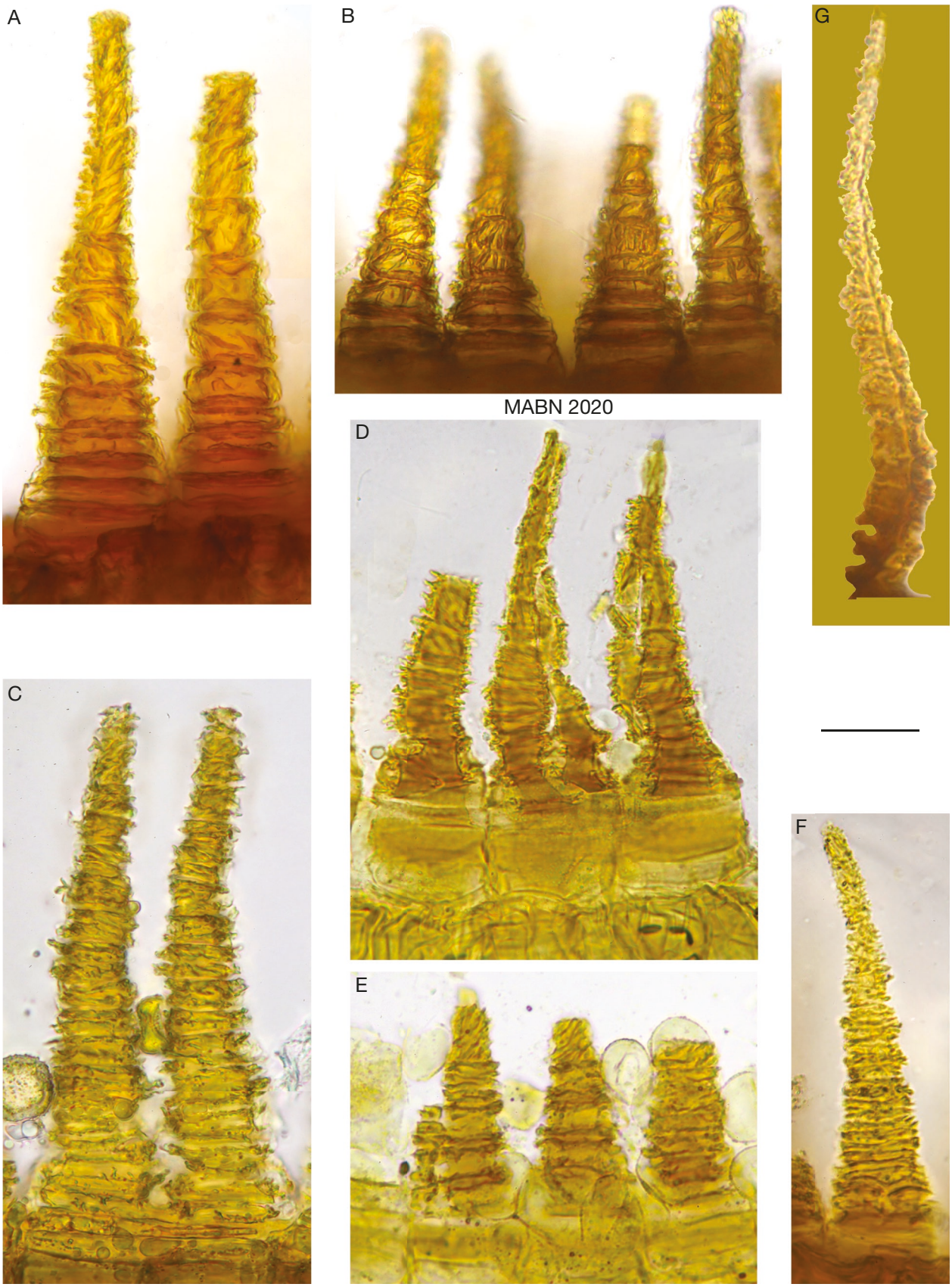

FIG. 11. — *Fissidens lagenarius* Mitt. **A**, OPL, note the transparent OPL lamellae protruding beyond the narrower underlaying IPL lamellae (left below); **B**, OPL; **C-F**, IPL variations: **C**, IPL of two teeth, each composed of a single column of half cells (reduced situation); **D**, three teeth focused on the incrassate lamellar plates; in the middle tooth two columns are clearly recognizable (normal situation); **E**, IPL of three teeth focused on the trabeculae; **F**, IPL of single tooth; **G**, side view of tooth. **A**-**D**, **G** from Brazil, São Paulo, *Yano 235*, SP, private herbarium Bruggeman-Nannenga; **E** from Zambia, North-western Province, Mushitu Forest, *Townsend 75/135*, E, private herbarium Bruggeman-Nannenga; **F** from Brazil, *Yano 560 235*, SP, private herbarium Bruggeman-Nannenga. Scale bar: 20 µm.

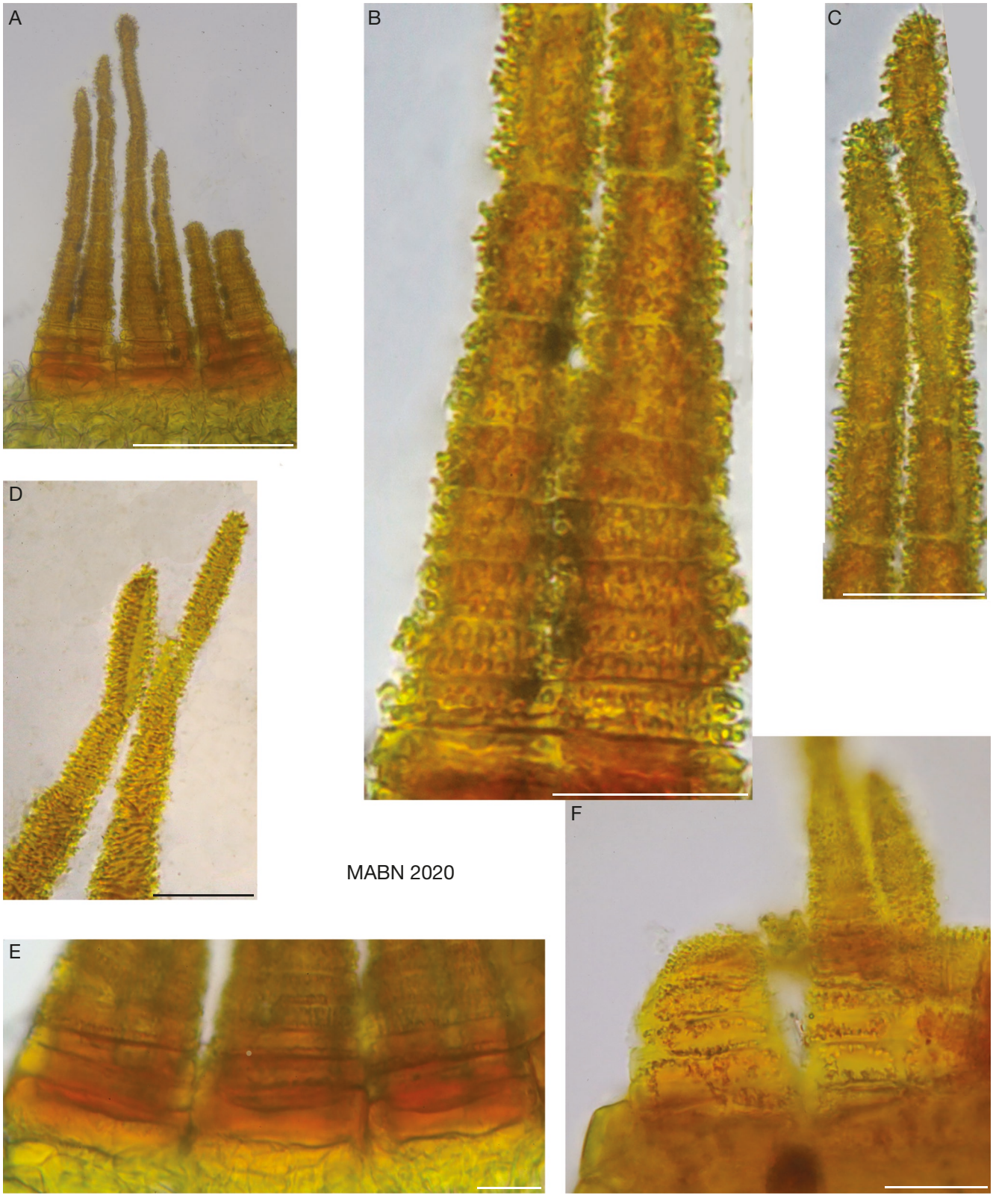

FIG. 12. — *Fissidens macroglossus* (Broth.) Brugg.-Nann. **A**, OPL of three deeply divided teeth; **B**, **C**, **E**, details of Fig. A; **D**, distal parts of filaments, partly in side-view; **E**, OPL basal cells; **F**, IPL basal part. **A**-**E** from Ivory Coast, Bonaké, *Porembski 33*, private herbarium Bruggeman-Nannenga; **F** from Cameroon, Bipindi Urwaltgebiet, *Zenker 2292*, isotype of *F. macroglossus*, private herbarium Bruggeman-Nannenga. Scale bars: A, 50 µm; B-F, 20 µm.

teeth, basal OPL lamellae with numerous, thin, high, close ridges and filaments spirally ornamented. It resembles *F. pocsii sensu lato*. The two differ in the relative width of leaves, those of *F. papillisetus* are 4-5 times as long as wide, those of *F. pocsii* are mostly wider, in

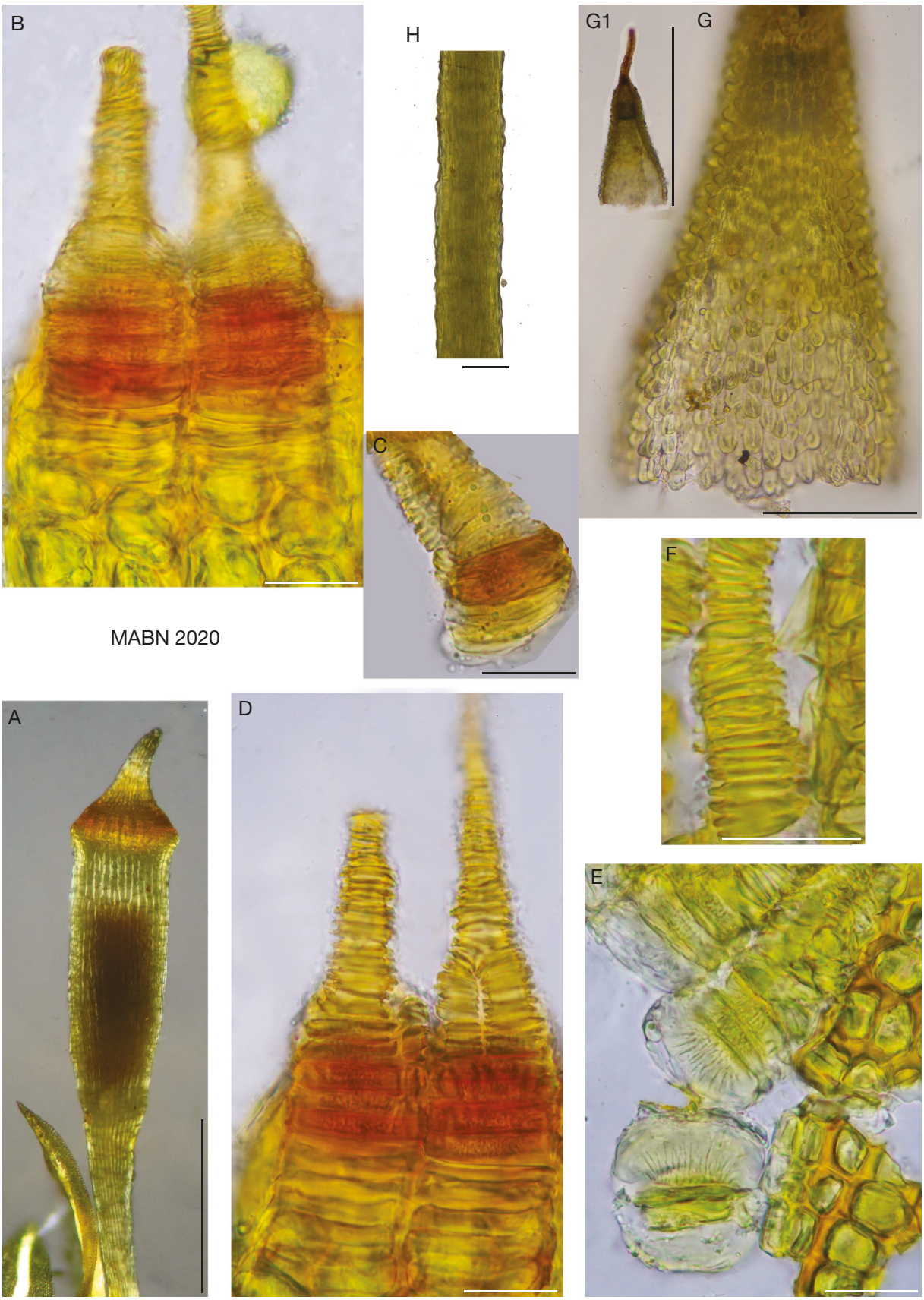

FIG. 13. — *Fissidens papillisetus* Brugg.-Nann. **A**, capsule with operculum; **B**, OPL of two teeth with spore; **C**, genuflexed basal part of tooth in side-view showing the high, close lamellar ornamentation; **D**, IPL of two teeth; **E**, detail of lamellar OPL ornamentation showing three free laying plates of which two with vertical striae on the right remnants of the operculum; **F**, "spiral" ornamentation of filaments; **G**, scabrose calyptra; **H**, papillose seta. All from Mauritius, Mt. Le Pouce, *Florins & Pócs 9538/B*, holotype: private herbarium Bruggeman-Nannenga, isotype: EGR. Scale bars: A, G1, 0.5 mm; B-F, 20 µm; G, 100 µm; H, 50 µm.

the margins of the vaginant laminae which are typically revolute in *F. pocsii* and plane in *F. papillisetus* and in the ornamentation of the basal OPL lamellae. In *F. papillisetus* this ornamentation consists of many close-packed, high, thin plates (Fig. 13B, C) and trabeculae hard to observe, whereas in *F. pocsii* the basal OPL trabeculae are distinct and the lamellar ornamentation is spaced and lower (Fig. 14A, D). The two species further have a different geographic distribution. Corticolous on branches.

DISTRIBUTION. — Endemic to Mauritius.

Peristome
Just above the insertion genu-flexed, undivided, ± 100 µm long (hard to measure), tooth base 25-33 µm wide.

Ornamentation
Basal OPL lamellae with thin, close-packed, high, striate plates (Fig. 13E) that are not or hardly distinguishable from the trabeculae (Fig. 13B, C); IPL with firm, close, horizontal to oblique ridges over almost the complete length (Fig. 13D); filaments "annular-spiral", becoming papillose near the apex.

Sporophyte
Seta 1.2-1.6 mm long, strongly papillose; capsule narrowly cylindrical, 0.5-0.65 × 0.2-0.25 mm, exothecial cell columns ± 32 columns, the cells linear-oblong; operculum short rostrate, 0.2-0.25 mm long; spores 16.0-25.5 µm, smooth.

Description and illustration
Bruggeman-Nannenga (in press: 40; fig. 3).

Fissidens pocsii Bizot & Dury ex Pócs *sensu lato* (Fig. 14)

Fissidens pocsii sensu lato is characterized by mammillose laminal cells, vaginant laminae with revolute margins, limbidia present on some or all leaves of perichaetial stems, leaves of vegetative stems limbate or not, antheridia in axillary buds as well as terminal, setae short, papillose. It is a rather heterogeneous species. It appeared, however, impossible to find differentiating features for its expressions. Differences in leaf shape, length of the costa, in anatomy of the stem, peristomes divided or undivided, growing on twigs or on bark of trees or large branches and geographical distribution appeared to be weakly or not correlated. Cross-sections of stems in this complex vary from round to elliptical, central strand present or not and walls of inner cells strongly incrassate (Fig. 14C) or thin. Corticolous on trees and twigs (Malagasy species on twigs).

DISTRIBUTION. — Tanzania, La Réunion and Madagascar.

Peristome
The peristome of this species is too variable to allow a description that is comparable to the other descriptions and does do justice to its variability. In Figure 14 a divided and an undivided peristome are shown. Peristomes of this species have "spiral" filaments. The peristome can be divided or not and the ornamentation of the basal OPL is variable. On the IPL the "spiral" ornamentation is not limited to the filaments but, like in *Fissidens papillisetus,* continues almost to the insertion (this feature, however, could not be checked in all specimens because of the poor quality of some peristomes). When undivided the peristome resembles that of *F. papillisetus* from which it differs by the OPL lamellae of the basal part: in *F. papillisetus* the lamellae are close packed (Fig. 13B, C) and in *F. pocsii* not (Fig. 14A, D). For further differences see *F. papillisetus.* When divided the peristome resembles that of *F. inclusus*. In *F. inclusus,* however, the IPL lamellae of the undivided part are smooth or have an inconspicuous ornamentation (Fig. 9C) whereas in *F. pocsii* there is a prominent ornamentation similar to that of the of the filaments (Fig. 14E). Furthermore, *F. inclusus* has shorter setae and limbidia that are restricted to the vaginant laminae of the upper perichaetial leaves.

Illustration and description
Bruggeman-Nannenga & Arts (2010: fig. 28).

Fissidens pseudoplumosus Bizot & Onr. ex Brugg.-Nann. (Fig. 15)

Fissidens pseudoplumosus is characterized by distant, scale-like leaves on the basal halves of the stems and linear-oblong to linear-lanceolate acute leaves on the upper halves, irregularly bistratose dorsal and apical laminae and limbidia restricted to the basal half of the vaginant laminae of upper and middle leaves of perichaetial plants. *Fissidens pseudoplumosus* has two subspecies. These have similar gametophytes and peristomes but differ in length of the setae and geographical distribution. *Fissidens pseudoplumosus* subsp. *pseudoplumosus* has very short 0.5 mm long setae and thus immersed capsules. It is known from *Réunion* where it grows on tree ferns and once collected from organic debris originating from a tree fern. Subspecies *subplanifrons* has longer, 1-2 mm long, setae and emergent to exserted capsules. It is known from Mauritius, Madagascar and the Comoro Islands Mwali and Ndzuani and also grows on tree ferns.

Peristome
± erect when wet, variable, irregularly divided or seemingly perforated, some teeth narrowing abruptly into a single filament, 120-250 µm long (hard to measure, often broken off), tooth base 32-38 µm wide.

Ornamentation
OPL basal 7-8 cells undivided, trabeculae smooth, papillose, well developed; proximal cells of the filaments with prominent, reticulate lamellar ornamentation (Fig. 15D, H); IPL basal undivided part with papillose trabeculae and smooth lamellae; lamellae of filaments thick plates (Fig. 15E); with high, close horizontal to oblique ridges (Fig. 15F), filaments "hemispiral" with close, oblique ridges present on the IPL but not on the OPL, apical part densely papillose on both layers. Characteristic of this peristome are irregularly divided teeth, relatively tall undivided parts and "hemispiral" filaments.

Sporophyte
Seta 0.5 mm in *Fissidens pseudoplumosus pseudoplumosus* and 1-2 mm in *Fissidens pseudoplumosus subplanifrons* (Bizot & Onr. ex Brugg.-Nann.) Brugg.-Nann. & Arts; capsule narrowly cylindrical, 0.7-0.9 × 0.3-0.4 mm, exothecial cell columns ± 32, the cells oblong; operculum unknown; spores 13-20 µm, ± smooth.

Description and illustration
For subsp. *pseudoplumosus*: Bruggeman-Nannenga & Arts (2010: fig. 30); for subsp. *planifrons:* (Bizot 1974: pl. 4); Bruggeman-Nannenga & Arts (2010: fig. 31).

Fissidens punctulatus Sande Lac.
(Fig. 16)

Fissidens punctulatus is characterized by broadly acute to obtuse leaves, costae that end 2-3(-6) cells below the leaf tips, unipapillose laminal cells, serrulate leaf margins, particularly on the vaginant laminae, short limbidia that are confined to the basal 1/3-1/2 of the vaginant laminae of the upper leaves of perichaetial plants, 1.0-2.5 mm long setae, and irregularly divided or undivided, papillose peristome teeth. Growing scattered between mosses and liverworts on bark.

DISTRIBUTION. — Paleotropics, Australia, widespread in Africa.

Peristome
± straight when dry, ± incurved when wet, undivided, seemingly perforated, teeth long, 150-220 µm long, tooth base 28-45 µm wide.

Ornamentation
OPL trabeculae recognizable, but indistinct (Fig. 16B), vertical walls not present, the two basal lamellae ± smooth, more distal ones coarsely papillose, no sharp distinction between basal part and filaments; IPL basal trabeculae well developed, double or not, mostly papillose, basal lamellae ± smooth, distal ones strongly incrassate and papillose (Fig. 16D1-3), distal OPL and IPL ± equally thick, papillose.

Sporophyte
Seta 1-2 mm long, smooth, capsule narrowly cylindrical, 0.5-0.7 × 0.25-0.35 mm, erect, with exothecial cell columns 32-40, of the cells oblong with thickened vertical walls; operculum 0.4-0.45 mm long; spores 14.5-17.5 µm, smooth to finely papillose.

Description and illustration
Renauld (1909: pl. 35, fig. 6 as *F. ligulinus* Müll.Hal.); Iwatsuki & Mohamed (1987: fig. 1 as *F. brevilingulatus* E.B.Bartram); Iwatsuki & Suzuki (1996: fig. IX); Bruggeman-Nannenga & Arts (2010: fig. 32).

Fissidens rotundifolius Brugg.-Nann.
(Fig. 17)

Fissidens rotundifolius is characterized by wide oblong-lingulate leaves with rounded obtuse apices and distally spurred costae that end 3-9 cells below the apex, firm-walled laminal cells that appear smooth, but are mammillose. It has undivided, small peristomes. Without a peristome it could be mistaken for *F. serratus* Müll.Hal. The two can be separated by the more distinctly serrulate margins (coarsely serrulate margins on the basal part of the vaginant laminae) and distinctly mammillose laminal cells of *F. serratus*. Furthermore, *F. serratus* has a *scariosus*-type peristome. – On bark sparsely mixed with *F. diaphanodontus.*

Peristome
Extremely small, incurved when wet, undivided; teeth ± 60-100 µm long, tooth base 23 µm wide.

Ornamentation
OPL four basal cells with smooth trabeculae that taper from the broad base to a thin edge*, lamellae* hard to observe, probably smooth, distal parts densely papillose; IPL trabeculae of basal part conspicuous, smooth; distal part with oblique ridges.

Sporophyte
Seta 1 mm long, smooth, basal part somewhat rugose; capsule cylindrical, 0.3 × 0.1.5-0.2 mm with exothecial cell columns 22-32, the cells oblong, thin-walled; operculum not seen; spores subglobose, 19-21.5 × 17-19 µm, papillose.

Description and illustration
Bruggeman-Nannenga (in press: 43; fig. 5).

Section *Neoamblyothallia* Tad.Suzuki & Z.Iwats.

Fissidens microcarpus Mitt. and ***F. imbricatus*** E.Britton & E.B.Bartram
(Fig. 18)

Fissidens microcarpus is characterized by oblong, lingulate, elimbate leaves, convex laminal cells and costae ending 10-20 cells below the broadly acute leaf apices. Corticolous, rupicolous and on soil.

DISTRIBUTION. — Tropical West Africa.

Peristome
Incurved when wet, undivided to irregularly divided, 130-170 µm long, tooth base (19.5-)23.5-45 µm wide.

The peristome of the corticolous *Fissidens microcarpus* differs hardly from ancestral *similiretis*-type. The OPL ornamentation of the undivided part is the same (compare Fig. 18A, D). The main differences are that it is irregularly divided to undivided and has shorter filaments with a papillose rather squamulose ornamentation (compare Fig. 18A, B with C).

Ornamentation
OPL trabeculae high and sharp, lamellae with a high, close ornamentation; filaments papillose with a few, indistinct squamulae.

Sporophyte
Seta 3 mm long, smooth; capsule cylindrical, 0.9 × 0.5 mm, slightly inclined, exothecial cell ± 66, the cells oblong, operculum 0. 4 mm long, spores (12.5-)14.5-20(-26.3) × 11.5-19.5 µm, papillose.

Description and illustration
Bruggeman-Nannenga & Pursell (1990: figs 32-42).

Remarks
In Figure 18 two species are illustrated: *Fissidens microcarpus* with a reduced peristome (Fig. 18A-C) and, for comparison,

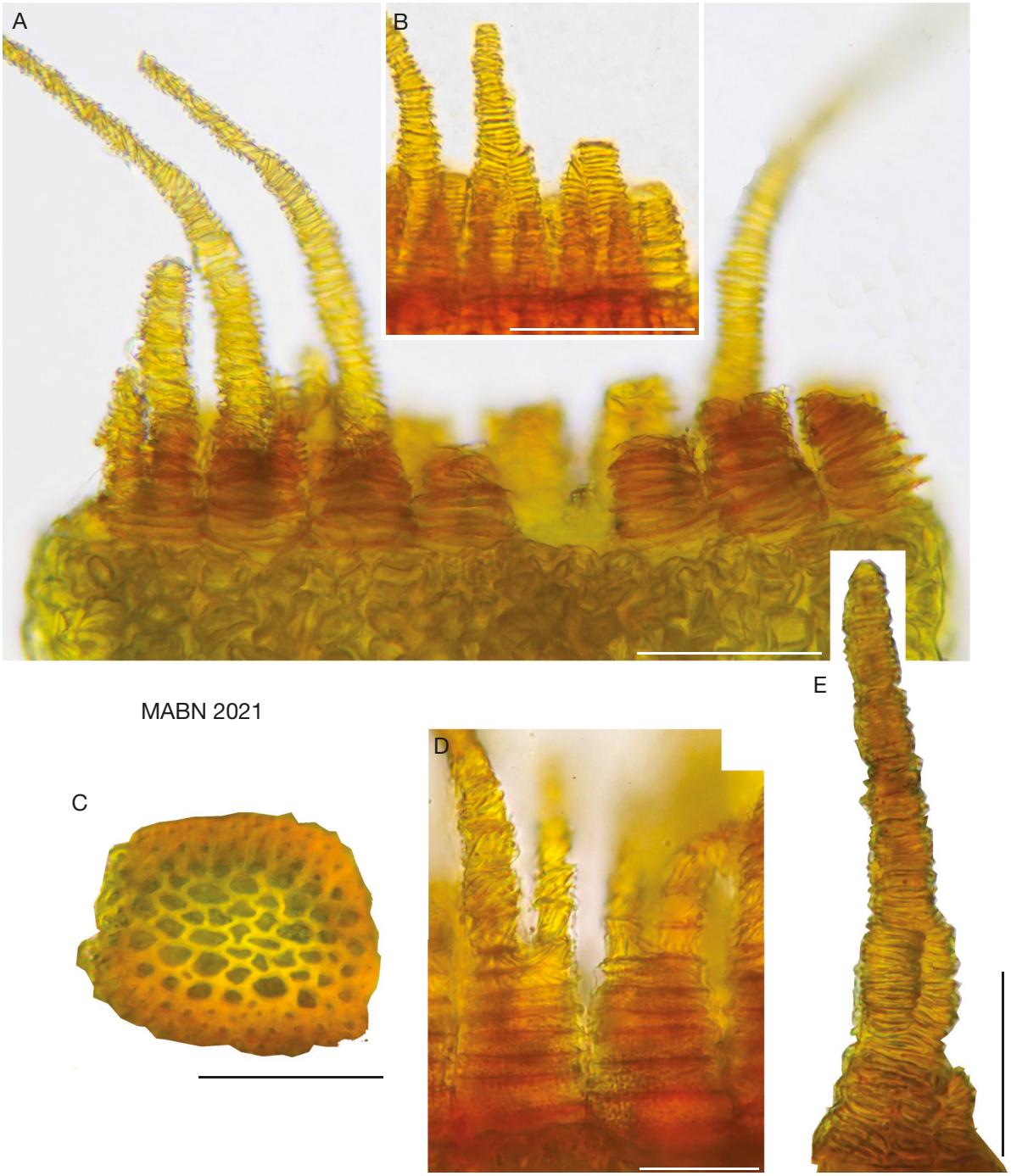

Fig. 14. — Pristome variations of *Fissidens pocsii* Bizot & Dury ex Pócs *sensu lato*. **A**, OPL, trabeculae clearly visible in side-view (on the right); **B**, IPL (basal parts somewhat obscured by overlaying OPL); **C**, stem cross-section; **D**, OPL two teeth (both divided); **E**, IPL (undivided tooth). **A**-**C** from Madagascar, Masoala Peninsula, *Pócs 9448/EB*, EGR, L; **D**, **E** from Madagascar, Bararake (Tsianovoha), *Heim 1348A*, PC0773826A. Scale bars: A-C, E, 50 µm; D, 20 µm.

F. imbricatus with a well-developed *similiretis*-type peristome (Fig. 18C, D).

Distribution and frequency of anomalous peristomes in the subgenera *Polypodiopsis*, *Neoamblyothallia* and *Fissidens*

Based on data from the papers by Fleischer (1904); Pursell (1987, 2007); Bruggeman-Nannenga & Berendsen (1990); Li & Iwatsuki (2001); Pursell & Bruggeman-Nannenga (2004); Suzuki & Iwatsuki (2007); Manjula *et al.* (2015); Beever *et al.* (2018); Suzuki *et al.* (2018); Bruggeman-Nannenga & Müller (2020) and as well as personal observations there appeared to be 54 species with imperfect peristomes in the subgenera *Polypodiopsis*, *Neoamblyothallia* and *Fissidens*, including 35 in subgen. *Polypodiopsis* (mainly *F.* sect. *Antennidens*), 17 *F.* subgen. *Fissidens* and two in *F.* subgen.

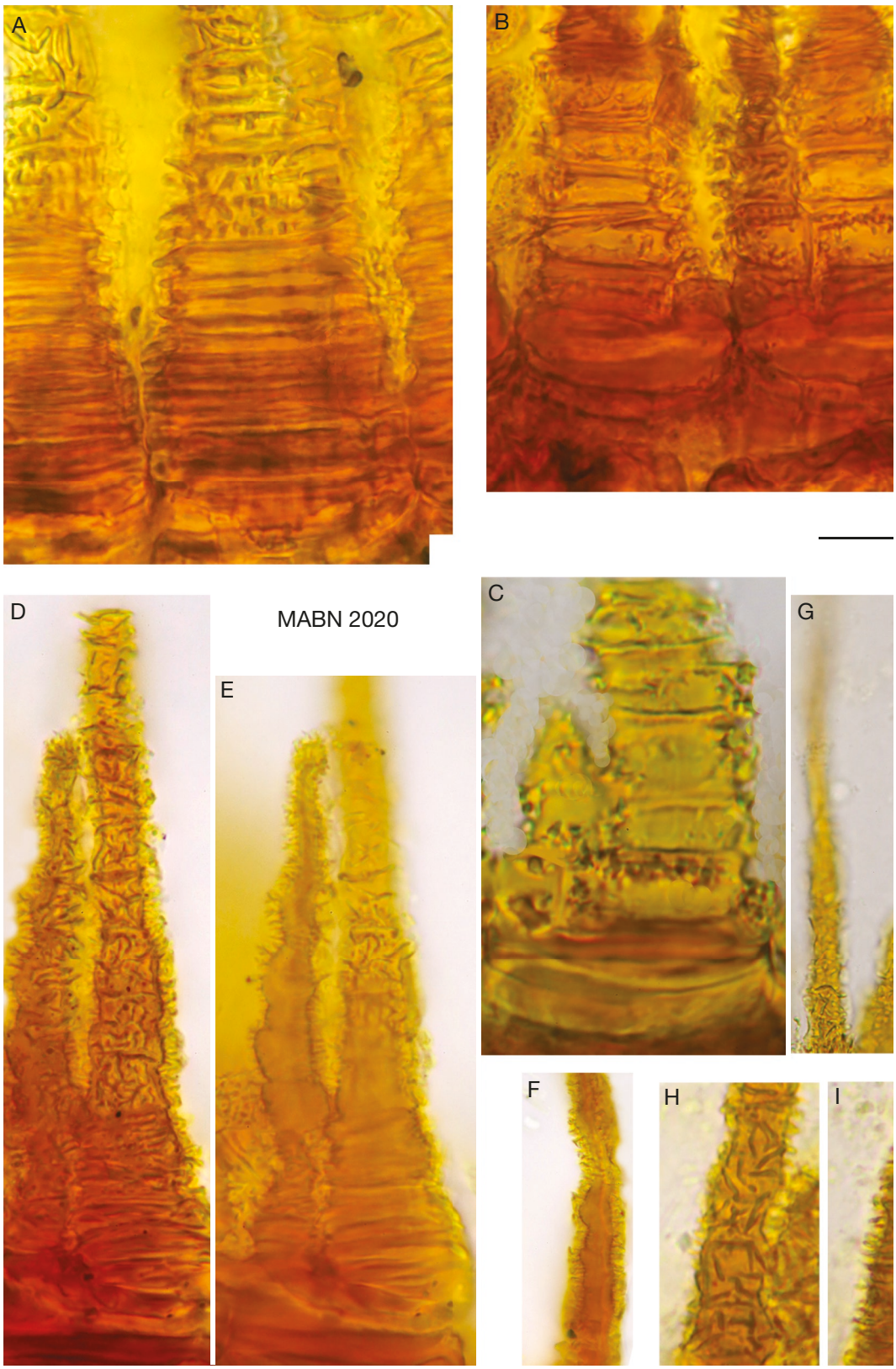

FIG. 15. — *Fissidens pseudoplumosus* Bizot & Onr. ex Pócs subsp. *pseudoplumosus*: **A**-**C**, **G**. **A**, OPL basal part and bifurcation; **B**, **C**, basal IPL, showing papillose trabeculae and smooth lamellae; **G**, papillose distal filaments. *F. pseudoplumosus* subsp. *subplanifrons* (Bizot & Onr. ex Brugg.-Nann.) Brugg.-Nann. & Arts: **D**-**F**, **H**-**I**. **D**, focused on the irregular somewhat reticulate OPL ornamentation; **E**, same tooth as Fig. D, but focused deeper to show the incrassate lamellar plates; **F**, side view basal part of tooth, OPL on the right; **H**, basal part of filament focus on OPL ornamentation; **I**, same tooth as Fig. H, focused on the "hemispiral" IPL ornamentation of high, dense oblique ridges. **A**, **B**, **G** from La Réunion, La Grande Montagne, Route Forestière de la Plaine d'Affouche, *Arts REU122-38*, BR, private herbarium M.A. Bruggeman-Nannenga; **C** from La Réunion, eastern slope of Piton de la Fournaise, sentier de la Ravine du Tremblet, *Onraedt 9378*, PC, type of *F. pseudoplumosus*; **D**-**F**, **H**-**I** from Mauritius, Shoulder of the Ponce (subsp. *subplanifrons*), *Ayres s.n.*, type of subsp. *subplanifrons*, BM. Scale bar: 20 µm.

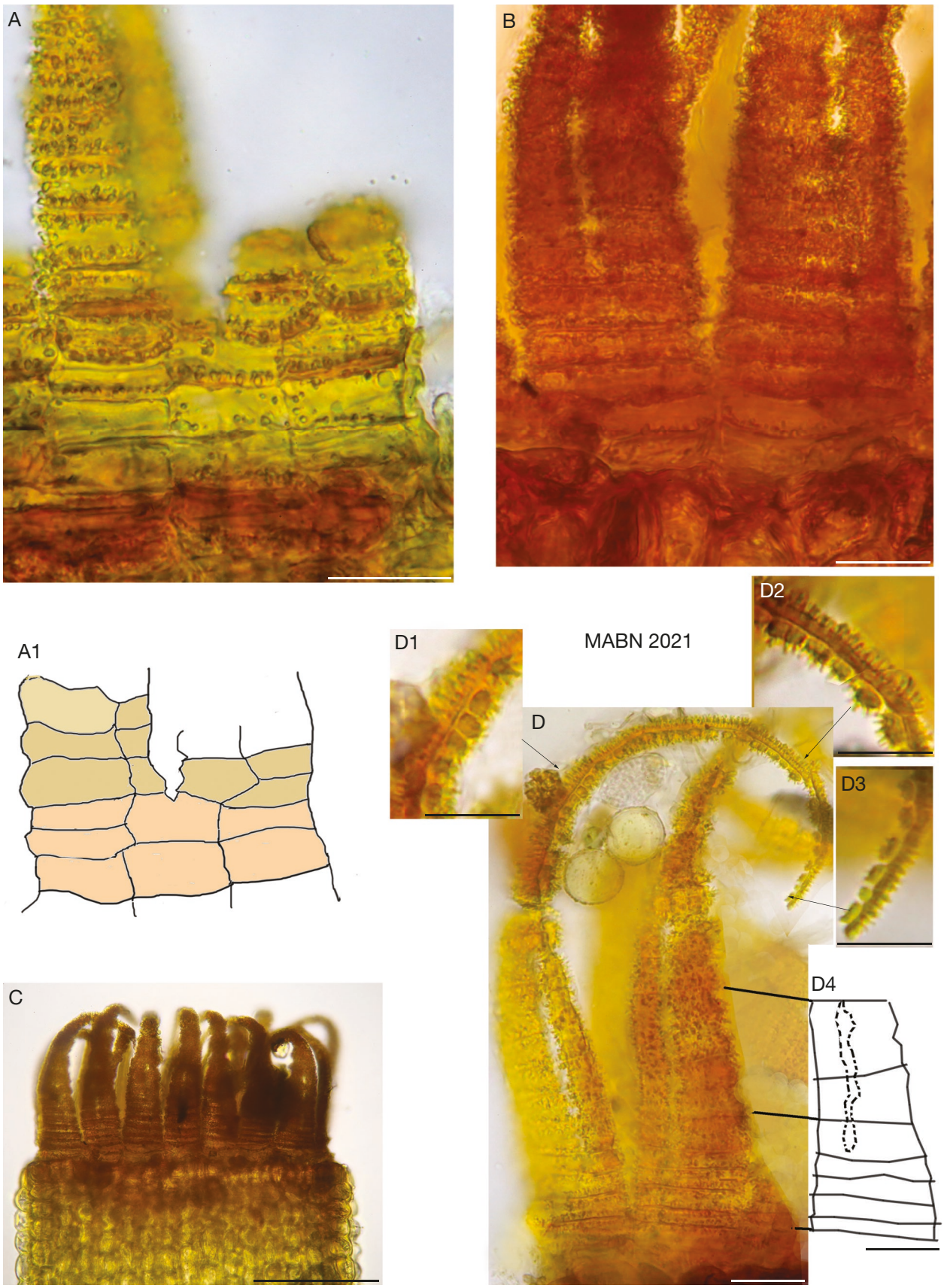

FIG. 16. — *Fissidens punctulatus* Sande Lac. **A**, basal IPL of pair of teeth; **A1**, line drawing showing the arrangement of cells in Fig. A . The part below the splitting (pale orange) is the continuation of the teeth on the inner surface of the capsule; **B**, basal OPL; **C**, capsule with slightly incurved peristome; **D**, pair of teeth with two spores; **D1-3**, details showing strongly incrassate IPL lamellae; **D4**, line drawing showing the single column of OPL cells, the dotted line marks the "perforations" that are probably just thin areas. All from Madagascar, Fôret d'Amboapaka, env. De Vohipeno, sur tronc mort, *Heim s.n.*, PC773871. Scale bars: A, B, D-D4, 20 µm; C, 100 µm.

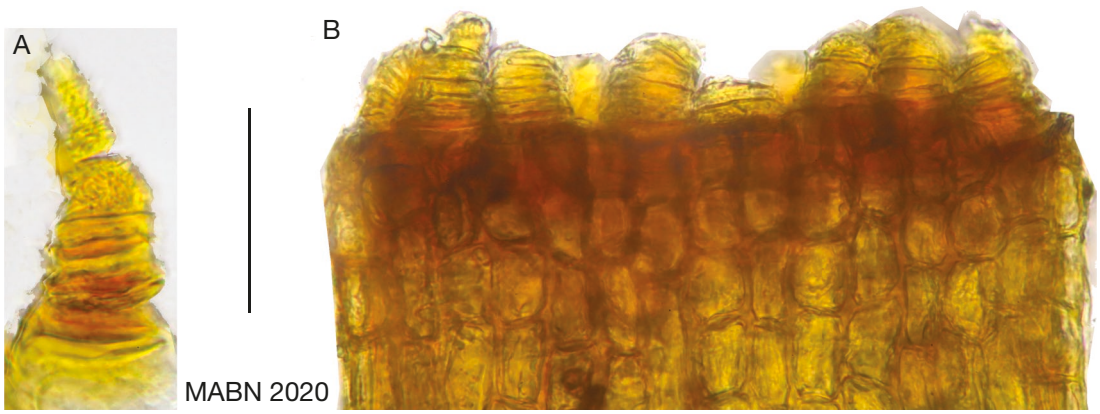

Fig. 17. — *Fissidens rotundifolius* Brugg.-Nann. **A**, OPL; **B**, capsule mouth with peristome teeth. Both from holotype: Tanzania, Hunga Valley below Amani, East Usambara Mts. *Pócs & Jones s.n.*, EGR, between *F. diaphanodontus*. Scale bar: 50 µm.

Neoamblyothallia. Differences were found between the subgenera. In *F.* subgen. *Polypodiopsis* and *F.* subgen. *Neoamblyothallia* most species with anomalous peristomes are (predominantly) corticolous (22 out 35 in *F.* subgen. *Polypodiopsis* and two out of two *F.* subgen. *Neoamblyothallia*); in *F.* subgen. *Fissidens* anomalous peristomes are common in aquatic species.

In the type subgenus of *Fissidens* species with anomalous peristomes often have deviant gametophytes. This was not observed in the other two subgenera.

DISCUSSION

This paper is about peristomes that morphologically do not conform to any of the main types (Pursell & Bruggeman-Nannenga 2004). Several are undivided or irregularly divided. In the past undivided and irregularly divided peristomes have been considered diagnostic for various genera and sections in the Fissidentaceae. Thus, the genera *Moenkemeyera* Müll. Hal., *Fissidentella* Cardot, *Sainsburia* Dixon, *Simplicidens* Herzog, *Octodiceras* Brid. and *Conomitrium* sect. *Sarawakia* Müll.Hal. were described. All these taxa are now subsumed under others (Pursell & Bruggeman-Nannenga 2004; Suzuki *et al*. 2018). Suzuki *et al*. (2018) included three species with anomalous peristomes in their molecular study. The epiphytic *Fissidens neomagofukui* Z.Iwats. & Tad.Suzuki and the aquatic *F. fontanus* (Bach.Pyl.) Steud. were resolved in *F.* subgen. *Fissidens* (characterized by a *bryoides*-type peristome), the third, *F. parkii* Mitt., in *F.* subgen. *Polypodiopsis* sect. *Antennidens* (in the tree as clade *Semilimbidium*).

Ancestral peristome types

As peristomes types play an important role in the definition of subgenera of *Fissidens*, species with anomalous peristome can be difficult to classify. For the subgenera in this paper this is not the case. *Fissidens* subgen. *Neoamblyothallia* is easily recognized by gametophytic traits and though *F.* subgen. *Polypodiopsis* is essentially based on sporophytic traits, its sections are gametophytically based:

Fissidens subgen. *Polypodiopsis* is defined by: *bryoides*-type costae, capsules with ± 32 columns of exothecial cells on the circumference and *scariosus*-type peristomes. It is supported by results of molecular analyses (Suzuki *et al*. 2018).

Sect. *Polypodiopsis* with ecostate leaves.

Sect. *Antennidens* with leaves typically semilimbate, less often elimbate or completely limbate, laminal cells small to medium-sized, pluripapillose, mammillose or rarely smooth (AL, see also sect. *Aloma*) and costa *bryoides*-type. This concept includes Brotherus' sections *Semilimbidium*, *Pycnothallia*, *Crenularia*, *Aloma* p.p. and clade *Semilimbidium* of Suzuki *et al*. (2018). It is the largest section in the Fissidentaceae.

Sect. *Areofissidens* with mid-dorsal laminal cells 30 or more µm long, leaves limbate in most species, laminal cells smooth or mammillose and costa *bryoides*-type.

Sect. *Aloma*. The tree of Suzuki *et al*. (2018) upsets the traditional circumscription of sect. *Aloma* and thus small species with smooth cells and weak or lacking limbidia can only be classified with molecular data. They can be either sect. *Antennidens* or sect. *Aloma*. Both are sections in subgen. *Polypodiopsis* so this has no impact on the peristome which is a *scariosus* type in both.

Fissidens subgen. *Neoamblyothallia* is defined by medium sized to large plants, elimbate leaves, leaves costate, costa *oblongifolius* type, capsule with more than 40 cells on the capsule periphery, peristome *similiretis*-type.

Based on their gametophytes the species of Figures 1-18 are classified as *Fissidens* subgen. *Polypodiopsis* (Figs 1-17) and *F.* subgen. *Neoamblyothallia* (Fig. 18). Thus the expected peristomes for these species would be the *scariosus* type and the *similiretis*-type and therefore we assume these to be ancestral types of these anomalous peristomes.

Comparison with the ancestral type

Generally, peristomes of corticolous species differ from the ancestral type by having shorter, narrower teeth with a different ornamentation. Unlike in the *scariosus*-type, there is mostly no abrupt change in ornamentation at the bifurcation and the teeth are less hygroscopic. Similar differences are seen in the peristomes of epiphytic species in other bryophyte groups (Vitt 1981).

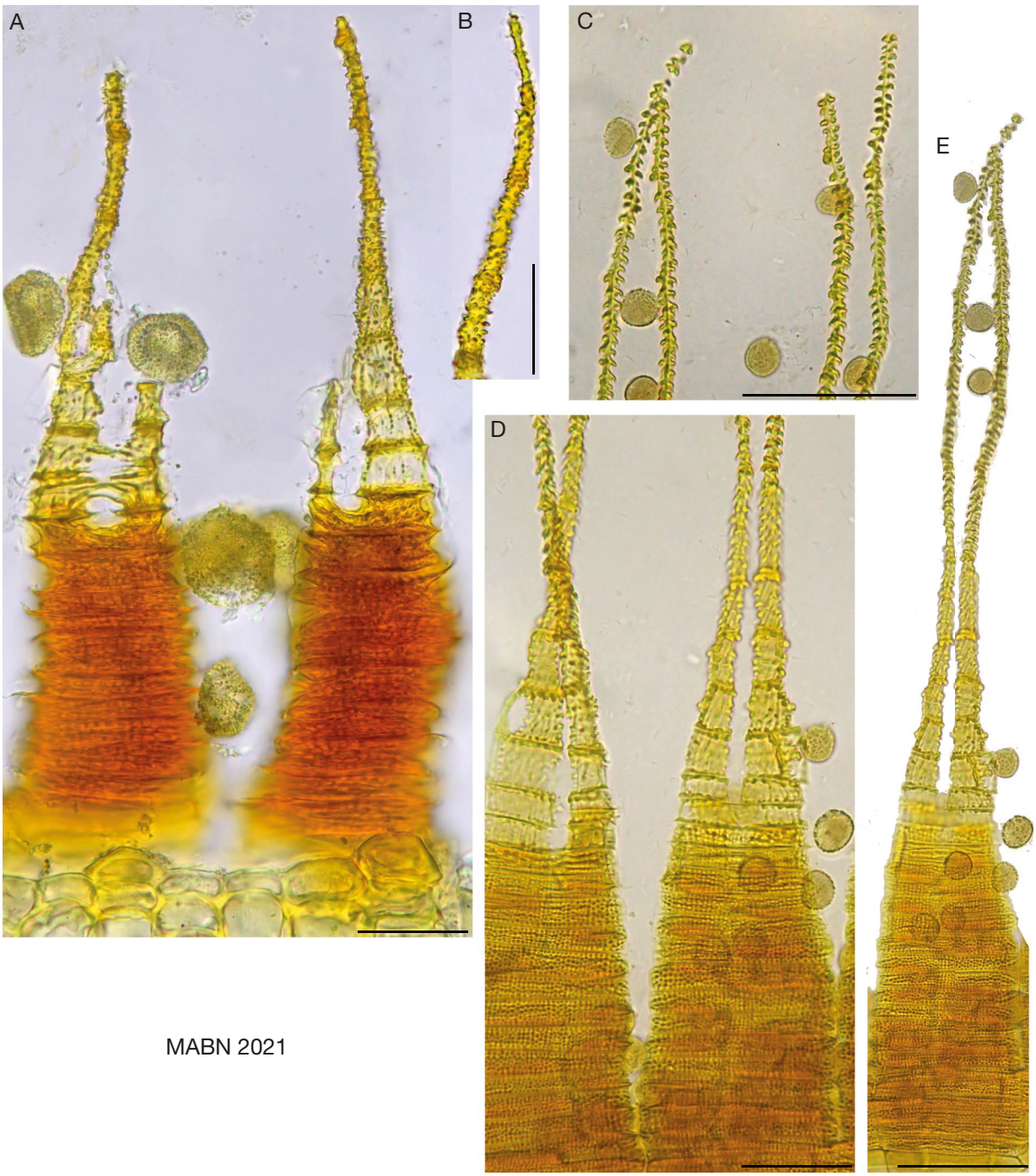

FIG. 18. — *Fissidens microcarpus* Mitt. **A**, OPL two peristome teeth; **B**, distal filament. *F. imbricatus* E.Britton & E.B.Bartram; **C**, squamose distal filaments; **D**, OPL undivided basal part and bifurcation; **E**, complete tooth OPL. **A**, **B** from Ivory Coast, Umgebung der Ortschaft Gouedie (= Gouele), *Müller E205*, DRE, private herbarium Bruggeman-Nannenga; **C**-**E** from Sullivant, Musci Cubensis 21, isotype, PC. Scale bars: A, B, 20 µm; C-E, 50 µm.

The ancestral *scariosus*-type peristome (Fig. 1) has been elaborately discussed and illustrated by Bruggeman-Nannenga (2021). It is characterized by: 1) teeth in the upper half divided into two filaments; 2) filaments with a "spiral" ornamentation (Fig. 1C); 3) undivided part: OPL lamellae with close-packed, horizontal ornamentation about as high as the trabeculae (Fig. 1B); 4) OPL cells around the bifurcation surrounded by a wall (Fig. 1A, B); 5) OPL cells at the base of the bifurcation torn into two halves that bend outwards towards each other (Fig. 1A, B); and 6) the filaments are strongly hygroscopic.

The first character, teeth divided is retained in *Fissidens arboricola*, *F. aristifer*, *F. inclusus*, *F. macroglossus*, some specimens of *F. pocsii sensu lato* and in *F. pseudoplumosus*. *Fissidens gardneri* can have irregularly divided or undivided peristomes. *Fissidens cyathaeicola* has undivided teeth, but

rudimentary second filaments (Fig. 5C) can be present. Undivided teeth are seen in *F. diaphanodontus*, *F. granulidens, F. jonesii*, *F. lagenarius*, *F. papillisetus*, some specimens of *F pocsii sensu lato* and *F. rotundifolius*. Some species, e.g. *F. ah-pengae* and *F. punctulatus* have irregular peristomes that look perforated, but without SEM it is impossible to be sure, whether apparent perforations are merely thinner areas or are true perforations.

The second character, filaments spirally ornamented is retained in *Fissidens arboricola*, *F. aristifer*, *F. inclusus*, *F. papillisetus*, *F. pocsii sensu lato*, but is lacking to indistinct in *F. ah-pengae*, *F. cyathaeicola*, *F. diaphanodontus*, *F. gardneri*, *F. granulidens*, *F. jonesii*, *F. lagenarius*, *F. macroglossus*, *F. pseudoplumosus*, *F. punctulatus* and *F. rotundifolius*. In the ancestral type, the IPL ornamentation of the undivided, basal part is quite distinct from the "spiral" ornamentation of the filaments. The same is seen in *F. inclusus* and in the type specimen of *F. aristifer*. In *F. arboricola*, *F. papillisetus* and *F. pocsii sensu lato*, however, the "spiral" ornamentation of the filaments occurs also on the IPL (but not on the OPL) almost to the insertion of the (undivided) basal part.

The third character, basal OPL lamellae with a conspicuous, high, close-packed horizontal ornamentation has been retained in *Fissidens papillisetus* only. Characters 4 and 5 have been lost in all species and character 6, filaments are strongly hygroscopic was not extensively studied, but appears to be diminished in all species.

Hygroscopic movements

Mueller (1973) studied the peristome of *Fissidens limbatus* (*bryoides*-type). Peristome movements are caused by changes in air humidity. He distinguished three different movements that occur almost simultaneously, a twisting of the filaments, a bending inwards of the filaments from the bifurcation so that they make an angle with the main axis and a bending towards the center of the capsule of the whole tooth from the base. Mueller found the last movement to be caused by differences in the uptake of moisture by the OPL and IPL of the basal, undivided part which result in differences in swelling in the two layers. The movements of the filaments are caused by changes in the orientation of microfibrils. Filament movements in the Fissidentaceae were studied by Ishihara & Iwatsuki (1992). These authors found the filaments of the *fissidens*-type of peristome (this includes both the *bryoides*- and *scariosus*-type) to be able to make strong hygroscopic movements.

Hygroscopic movements in the African corticolous species

The peristomes of corticolous species are mostly undivided or have short, often stiff filaments. In most species the movement is more or less restricted to a bending of the whole tooth which, when moistened, straightens with the upper parts (divided or not) erect or gently curved inwards, but not making a distinct angle with the main axis. This differentiates them from the *scariosus*-type in which the filaments bend inward making an angle with the main axis at the bifurcation when moistened.

The case of the "*bryoides*-type of peristome" of *F. inclusus*

The peristome of this species looks like a weak *bryoides*-type peristome. This type is characteristic of *Fissidens* subgen. *Fissidens*. Species of this subgenus have leaves with limbidia on all laminae, smooth laminal cells and 40 or more exothecial cells around the capsule circumference. *Fissidens inclusus,* however, has mammillose cells, limbidia restricted to the vaginant laminae and ± 32 columns of exothecial cells around the capsule. These features firmly place it in *F.* subgen. *Polypodiopsis.* Like the peristomes of many corticolous species the *bryoides*-type peristome differs from the *scariosus*-type in characters 3, 4 and 5. The resemblance to the *bryoides*-type is due to the nature of the lamellar ornamentation that in *F. inclusus* has become papillose and in other corticolous species reduced, but mostly not papillose. The resemblance to the *bryoides*-type of peristome is most likely incidental.

Other sporophytic characters

During this study it appeared that as a rule corticolous *Fissidens* species have short, often papillose setae and shorter, narrower and less hygroscopic teeth than non-epiphytic species. This concurs with what is seen in other groups of bryophytes (Vitt 1981).

Vitt (1981) listed several traits that are frequent in corticolous species: short, straight often stout setae; erect, oblong to ovate, sometimes strongly ribbed capsules that are often emergent from enlarged perichaetial leaves and/or have large calyptrae; and reduced or even absent peristomes. Several of these features are also found in corticolous species of *Fissidens.* Nearly all species discussed in this paper have short, up to 1.5 mm long, often papillose setae, (narrowly) cylindrical capsules with a small mouth (which corresponds with the narrow peristome teeth) and reduced peristomes. Deeply divided, narrow, scarcely hygroscopic peristomes will obviously influence spore dispersal. Opercula of corticolous species are typically shorter (0.2-0.3 mm versus (0.3-)0.4-0.6(-0.7) mm) than in non corticolous species of sect. *Antennidens*. An exception is *F. punctulatus* with opercula 0.45-0.55 mm long. Since the peristome is produced by the inner layers of the operculum it is not unexpected that species with short peristomes also have short opercula.

To investigate whether spore size is affected by a corticolous lifestyle in *Fissidens* I compared the spore sizes of *F.* subgen. *Polypodiopsis* given by Iwatsuki & Suzuki (1982), Pursell (2007) and Bruggeman-Nannenga (2017) with the spore size of the species discussed in this paper. It appeared that most *F.* subgen. *Polypodiopsis* species have spores between 7-20 µm in diameter. Thus spores up to 20 µm may be regarded as "normal". Only a few corticolous species appeared to have very large spores. *Fissidens brevipes* Besch., a corticolous, neotropical species has spores 20-27 µm in diameter (Pursell 2007) and the corticolous Indian *F. macrosporus* Dixon has spores of 27-30 µm in diameter. Most corticolous African species with reduced peristomes have spores that fall within the categories "normal" or "intermediate". Large spores were found in the pantropical *F. gardneri* (spores 22.5-34.5 µm),

the Malagasy *F. arboricola* (spores 23.5-32.5 µm) and the Tanzanian *F. inclusus* (17.5-)19-25(-28) × 15.5-23 µm).

Gametophytic characters

The species in this paper do not have anomalous gametophytes. Excepting that stems consisting of incrassate cells (Fig. 14C) are frequent in corticolous, but not in non corticolous species, there we found scarcely any differences between gametophytes of corticolous and non-corticolous species.

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