

Studies in the liverwort genus *Fossombronia* (Metzgeriales) from southern Africa. 1. Three new species from Northern Province, Gauteng and Mpumalanga

S.M. PEROLD*

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ABSTRACT

Three new species of *Fossombronia* from Northern Province, Gauteng and Mpumalanga (formerly Transvaal) are described: *F. gemmifera*, *F. glenii* and *F. straussiana*. *F. gemmifera* is distinguished by a highly convoluted pseudoperianth, the frequent presence of gemmae produced dorsally on the stem, lamellate spores and mostly rather short elaters; *F. glenii* can be recognized by a smallish, deeply lobed pseudoperianth, perigonal bracts with finger-like projections shielding the antheridia and by spinous spores; *F. straussiana* is distinct by its hyaline or brownish rhizoids, by its dense, frilly leaves, its pseudoperianth with lamellate lateral outgrowths, by spore ornamentation that usually has inclusions in the incomplete areolae and by the elaters which are finely papillose.

INTRODUCTION

Within the order Metzgeriales the cosmopolitan simple-thalloid liverwort genus *Fossombronia* Raddi is classified in the subfamily Fossombroniaceae Engl. emend. R.M.Schust. (family Fossombroniaceae Hazsl. (= Codoniaceae H.Klinggr.). The Fossombroniaceae is the only family under the suborder Fossombroniineae R.M.Schust. and is regarded as phylogenetically pivotal (Solomon 1995). It comprises four genera: *Petalophyllum* Nees & Gottsche ex Lehm., *Sewardiella* Kashyap, *Austrofossombronia* R.M.Schust. and *Fossombronia*, of which only the latter is known to occur in southern Africa.

Plants of the genus *Fossombronia* are small, usually gregarious with mostly prostrate, fleshy stems, laterally bearing succubously inserted, undulating or crisped thallus wings, dissected into leaf-like segments and free to the base, where they are bistratose, but unistratose elsewhere. The stems are anchored to the substrate by rhizoids which are usually purple, but hyaline in a few rare species.

The gametangia develop acropetally and are situated dorsally along the stem between the leaf insertions. They are either intermingled or borne on separate shoots in monoicous species, or they may occur on separate plants in dioicous species. The antheridia are short-stalked, ± globose and either naked or shielded by perigonal bracts. The archegonia are exposed, but after fertilization the developing sporophyte becomes surrounded by a campanulate pseudoperianth, constricted at the sometimes stipitate base, and flaring at the plane, lobulate or crispate mouth. The globose capsule is raised on a moderately short or long seta, 6 or 7 to 10 cells in diameter; the capsule wall is bistratose, the outer wall with delicate, hyaline cells and the inner wall with irregularly quadrangular cells, containing nodular and semi-annular thickenings. The walls rupture irregularly into small plates, releasing the spores and

elaters. The spores are relatively large and highly ornamented with spines, lamellae or areolae. The ornamentation on the outer face is generally considered species-specific and regarded as essential for identification, although 'so variable that patterns of ornamentation . . . must be used to define taxa' (Schuster 1992). The elaters may be well or occasionally poorly developed and are usually 2- or 3-spiral. The determination of sterile material is extremely difficult, if not impossible because of the plasticity of the gametophytes, the morphology of which varies considerably according to environmental conditions.

HISTORICAL NOTES

The genus *Fossombronia* has been relatively poorly studied in southern Africa. Lehmann (1829) described *Fossombronia* (sub *Jungermannia*) *leucoxantha*, collected by Ecklon on Table Mountain, Devil's Peak and Lion's Head and also reported the presence of *F.* (sub *Jungermannia*) *pusilla* L. on Table Mountain. Gottsche *et al.* (1844–1847) confirmed the presence of *F. pusilla* Nees and described *F. crispa* Nees from Promontorio Bonae Spei. Krauss (1846) reported *F. angulosa* 'in rupibus rivulorum montium natalensium'. Mitten (1878) described *F. tumida* collected by the Rev. A.E. Eaton at the foot of Lion's Head and endorsed the records of *F. crispa* and *F. leucoxantha* from localities near Cape Town. Stephani (1900) described *F. zeyheri* and *F. spinifolia*. Sim (1926) added no new species, but Arnell (1952) described three from the Cape: *F. capensis*, *F. densilamellata* and *F. montaguensis* (Perold 1997: 29). Arnell (1963) stated that 'the South African species of the genus are in great need of revision'. Scott & Pike (1984, 1987a–c, 1988a, b), who studied the genus in Australia (i.e. the western parts of the State of Victoria and adjacent regions of South Australia and New South Wales) for six years and described many new species from there, expected a comparable species richness to emerge from a long-term study of the genus in South Africa (and South America), since they regarded its origins to have been mainly in Gondwanaland.

* National Botanical Institute, Private Bag X101, Pretoria 0001.
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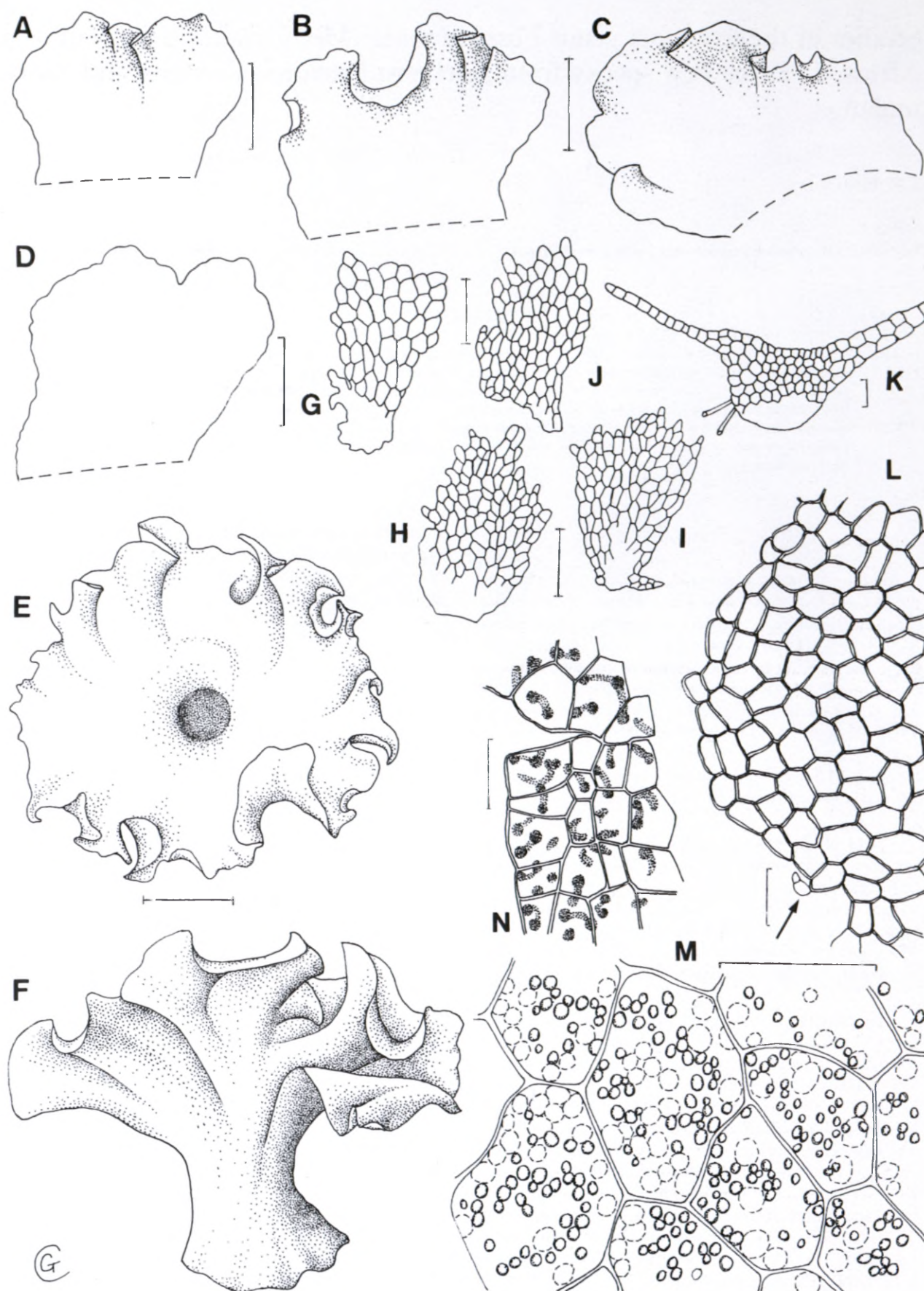


FIGURE 1.—*Fossombronina gemmifera*. A–D, leaves; E, opened pseudoperianth; F, pseudoperianth from side; G–J, perigonal bracts; K, cross section of stem; L, detail of marginal area of leaf, with slime papilla (see arrow); M, median leaf cells with oil bodies and chloroplasts; N, cells in capsule wall. A, D, Strauss & Retief CH13655; B, C, Perold & Koekemoer 3116b; E, F, Perold & Van Rooy 3559a; G–N, Strauss 132. Drawn by G. Condy. Scale bars: A–F, 500 μ m; G–J, 250 μ m; K, 100 μ m; L–N, 50 μ m.

This paper is the first of a series dealing with southern African *Fossombronia* species.

METHODS

Samples of field-collected specimens were transferred to a conically shaped fine-mesh sieve and washed in a jet of running water to clear away soil particles. Remaining particles were manually removed by using fine-tipped forceps. Cross sections were cut of some cleaned stems; several leaves and a pseudoperianth were detached and all transferred to a drop of water on a clean slide. Finally a coverslip was applied to the preparation, which was stored in a covered plastic dish lined with damp filter paper. During examination of the slide the evaporated water was periodically replenished. The structures were measured and also photographed under a compound light microscope.

The remaining portion of the cleaned specimen was fixed in FAA (formaldehyde/alcohol/glacial acetic acid and distilled water in proportion of 2:1:1:20). For later reference some thalli were permanently preserved in FAA, the remainder only for several hours and then dehydrated in an ascending series of acetone to 100% and critical point dried in a Balzers Union dryer, using liquid CO₂ as the transitional fluid. The thalli were mounted on aluminium stubs with double-sided Sellotape, gold-coated, then viewed and photographed, using an ISI SX 25 scanning electron microscope (SEM).

There are some advantages to studying and photographing *Fossombronia* material, treated as described above, with the aid of SEM. Scott & Pike (1984) stated that the form, colour and orientation of the leaves (of different species) are distinct but 'beyond our powers to illustrate and exceedingly difficult to describe'. Although the colour cannot be recorded by SEM, the form and certainly the orientation of the leaves can. Scott & Pike (1984) also observed that 'male plants have often shrivelled and disappeared by the time the corresponding spores are ripe and the gametophyte is then so desiccated that its pristine vegetative appearance is irrecoverable'. Samples taken at different stages and treated as above, would have made comparisons easier for them. Scott & Pike did not illustrate the plants of any of their new species, except *F. rudis* (Scott & Pike 1988b) and relied heavily on descriptions and the spore ornamentation to distinguish between species.

The spores and elaters were mounted on slides in Hoyer's fluid for examination and measurement by LM. For SEM microscopy some spores and elaters from the same capsule were allowed to air-dry, mounted on stubs with double-sided Sellotape, gold coated, viewed and photographed. SEM micrographs of *Fossombronia* spores have frequently been published and have been used as an aid to identification. Features of spore morphology should be used with caution, however, because they can be rather variable, and the spores need to be fully mature. The Degree Reference System was used for recording distribution data (Edwards & Leistner 1971).

1. *Fossombronia gemmifera* Perold, sp. nov.

Plantae repentes, gregariae vel dispersae; saepe gemmas dorsaliter secus caulem ferens. Folia imbricata, fimbriata, apicem versus aliquando longiora quam latiora, basin versus plerumque breviora quam latiora, nonnulla leviter bilobata, alia apicem versus undulata. Rhizoidea purpurea. Monoicae, interdum ut videtur dioicae. Antheridia bracteis tecta. Pseudoperianthium breviter setatum, orificio intricate convoluto, in lobis multis diviso. Sporae 55.0–62.5 µm diametro, superficie distali lamellis minimum 14 irregularibus duplicato-parietatis, aliquando areolas imperfectas facientibus; superficie proximali sine nota triradiata distincta, areolis imperfectis, parietibus altis circumcinctis. Elateres 100–160 µm longi, medio 7.5 µm lati, extremitates versus decrescentes, bis vel ter spirales, sed interdum arcte spirales, 50.0–62.5 µm longi, 12.5 µm lati.

TYPE.—Northern Province, 2427 (Thabazimbi): Kransberg, Farm Geelhoutbosch, on streambank, directly south of rondavel, (–BC), *S. Strauss* 132 (PRE, holo.). 2529 (Witbank): ± 80 km E of Pretoria, on Pretoria/Witbank road, facing Balmoral turnoff, left side of road at seepage area, (–CC), *Perold & Van Rooy* 3559a (PRE, para.).

Plants smallish to medium-sized, creeping, gregarious or scattered, green, proximal leaves sometimes clasped around stem, occasionally with pink margins; shoots simple, 5.0–9.0 mm long, 0.85 mm high, 2.6 mm wide, or once/twice furcate, apical segments moderately divergent (Figure 2A) 2.0–5.0 mm long, basally ± 3 mm long. Stems prostrate, in cross section apically 300–325 µm (12 or 13 cell rows) high, 400–500 µm wide, basally 250 × 300 µm, plano-convex (Figure 1K). Rhizoids purple, 12.5–20.0 µm wide, some with internal mycorrhizal hyphae. Leaves overlapping, frilly, obliquely inserted succubously, variously shaped, toward apex sometimes longer than wide, but more proximally usually shorter than wide, 925–1525 × 1325–1625 µm, some slightly bilobed (Figure 1A, D), others rufed above (Figure 1B, C); lateral margins with 3 or 4 uni- or bi-celled slime papillae (Figure 1L). Leaf cells thin-walled, at upper margins subquadrate to rectangular across, 32.5–50.0 × 22.5–30.0 µm, at lateral margins long-rectangular, up to 75 × 30 µm; upper laminal cells (4-)5- or 6-sided or polygonal, 32.5–50.0 × 22.5–30.0 µm, middle laminal cells 62.5–72.5 × 37.5–50.0 µm, basal cells 112.5–137.5 × 37.5–62.5 µm. Oil bodies glistening, 13–36 per cell, rounded, up to ± 3.5 µm in diameter; chloroplasts numerous, round or oblong, 5.0–7.5 µm in diameter (Figure 1M).

?Monoicous, some specimens with shoots bearing both antheridia and archegonia, but occasionally only antheridia or often only archegonia present. Antheridia dorsal on stem, interspersed between archegonia, short-stalked, globose, ± 185 µm in diameter, shielded by an irregularly shaped perigonial bract (Figure 2C), 500–700 × 380–450 µm, margins toothed, with projecting cells and slime papillae (Figure 1G–J), cells in interior 4–6-sided, 80.0–90.0 × 30.0–37.5 µm; sometimes antheridia in groups between leaves and then lacking bracts or with reduced bracts (Figure 2B). Archegonia numerous along stem, naked, up to 3 per shoot becoming fertilized, soon

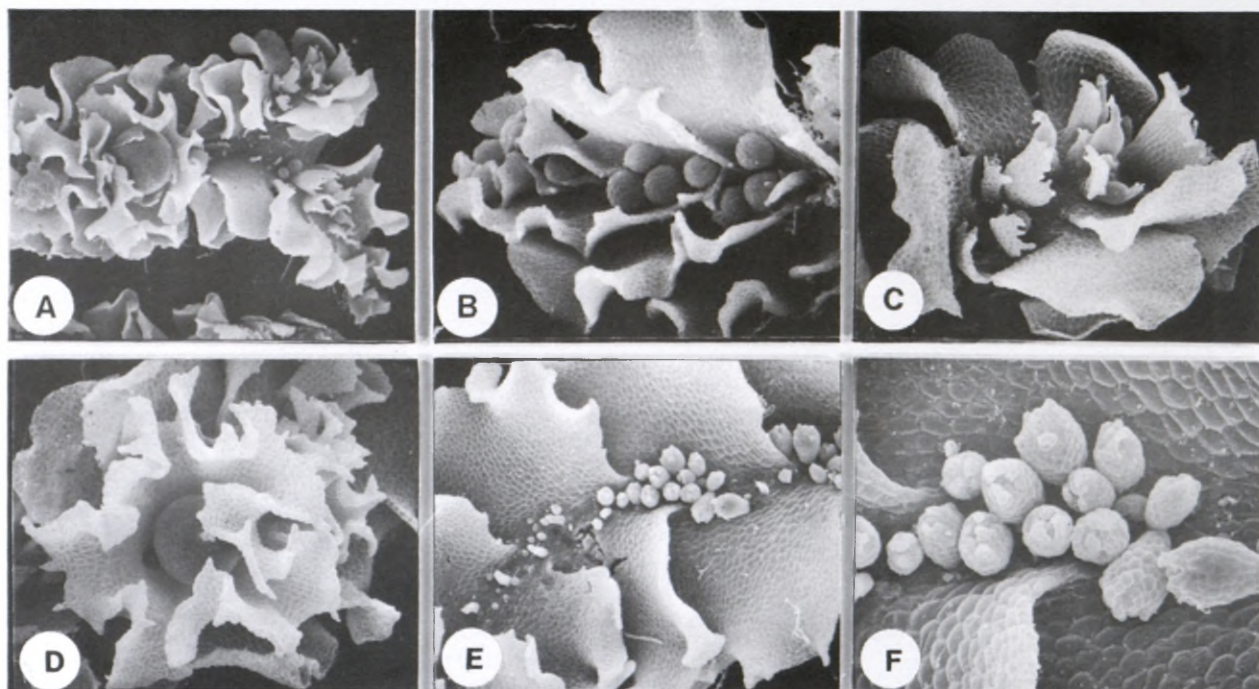


FIGURE 2.—*Fossombronina gemmifera*. A, stem branching near apex, bracts and pseudoperianth with capsule shown; B, antheridia between leaves; C, detail of perigonal bracts with mostly obscured antheridia and young fertilized archegonia; D, convoluted pseudoperianth from above; E, archegonia and gemmae between leaves; F, close-up of gemmae. A, C, D, Strauss 132; B, Perold & Koekemoer 3116b; E, F, Perold & Van Rooy 3557. A, $\times 13$; B, $\times 26$; C, $\times 21$; D, E, $\times 20$; F, $\times 54$.

forming young pseudoperianths. *Pseudoperianths* often crowded together, in acropetal sequence, raised on a short stalk, $\pm 210 \times 470 \mu\text{m}$, widely flaring above (Figure 1F), $\pm 900 \mu\text{m}$ long, up to $2000 \mu\text{m}$ wide across intricately convoluted mouth (Figure 2D), divided into numerous lobes (Figure 1E), $200\text{--}500 \times 150\text{--}440 \mu\text{m}$, some apically rounded, others with an acute apex ending in a papilla; cells comparable in shape and size to those of leaves. *Capsules* globose (Figure 2D), up to $\pm 600 \mu\text{m}$ in diameter, enveloped in a calyptra which is later shed, capsule wall bistratose, cells in inner layer irregularly shaped, $27.5\text{--}50.0 \times 25.0\text{--}37.5 \mu\text{m}$, each cell wall with (1)2–4 nodular and occasionally semi-annular thickenings (Figure 1N). *Seta* delicate, $1.2\text{--}3.2 \text{ mm}$ long, $270\text{--}350 \mu\text{m}$ in diameter, 6 cells across. *Spores* brown, hemispherical (Figure 3C), $55.0\text{--}62.5 \mu\text{m}$ in diameter, including lamellae projecting around circumference, distal face convex (Figure 3A, B), with at least 14 irregular, mostly double-walled lamellae running across, $\pm 7.5 \mu\text{m}$ apart, occasionally anastomosing and forming incomplete areolae; proximal face (Figure 3D, E) lacking distinct triradiate mark, ornamentation seemingly 'raised' from an encircling, marginal furrow (Figure 3E), tall walls forming small, irregular, incomplete areolae, up to $5 \mu\text{m}$ wide, around periphery 19–22 projecting 'ends' of lamellae, $\pm 5 \mu\text{m}$ long. *Elaters* (Figure 3F) yellow-brown, smooth, mostly rather small and sometimes poorly formed, $(50.0\text{--})62.5\text{--}85.0 \mu\text{m}$ long, medianly $12.5 \mu\text{m}$ wide, 3(–4)-spiral and loosely coiled, tapering toward tips, $5 \mu\text{m}$ wide and ending in bispiral loops, rarely $100\text{--}160 \mu\text{m}$ long, $7.5 \mu\text{m}$ wide medianly, 3-spiral. *Vegetative reproduction* by gemmae (Figure 2E, F), abundantly borne dorsally along stem, short-stalked, spindle-shaped, up to $300 \times 170 \mu\text{m}$, green when fresh, turning brown with age.

Fossombronina gemmifera grows on sandy loam soil on stream banks or at seepages, often mixed with mosses or

other *Fossombronina* species, particularly *F. straussiana*, which has hyaline rhizoids and is thus easily distinguished from it. This new species is quite distinctive with its highly convoluted pseudoperianth and by the frequent presence of dorsal gemmae for which it has been named. Its spore ornamentation with double-walled lamellae on the distal face and 'raised' on the proximal face above a clear marginal furrow, is also unique. There are two other species with purple rhizoids from the same distribution area: *F. glenii* which has spinous spores and *F. zeyheri* which has reticulate spores. *Fossombronina gemmifera* has been collected at several localities in Northern Province and Gauteng (Figure 4).

2. *Fossombronina glenii* Perold, sp. nov.

Plantae repentes, gregariae vel crebrae in coloniis. *Folia* imbricata, undulata, valde obliquiter inserta, plerumque oblonga, longiora quam latiora, apicem versus latiora quam basi, apice subtruncata, lobis vadosis, angulatis. *Rhizoidea* purpurea. Dioicae. *Antheridia* bracteis cum laciniis digitiformibus tecta. *Pseudoperianthium* infundibuliforme, orificio in lobis pluribus diviso, aliquot ad basin divisus. *Sporae* $40.0\text{--}52.5 \mu\text{m}$ diametro, superficie distali cum spinis multis altis conicis, raro fractis vel cristis brevibus junctis; superficie proximali sine nota triradiata distincta, cum tuberculis multis tenuibus vel grossis inspersis. *Elateres* $70.0\text{--}137.5 \times 7.5\text{--}10.0 \mu\text{m}$, bis vel ter spirales.

TYPE.—Northern Province, 2427 (Thabazimbi): Waterberg, Welgevonden Estate, cliffs at drift over Sterkstroom above farmhouse, in partial shade, with *Fissidens erosulus* (Müll.Hal.) Paris, (–BD), H.F. Glen 2146 (PRE, holo.); H.F. Glen 2134, same locality (PRE, para.).

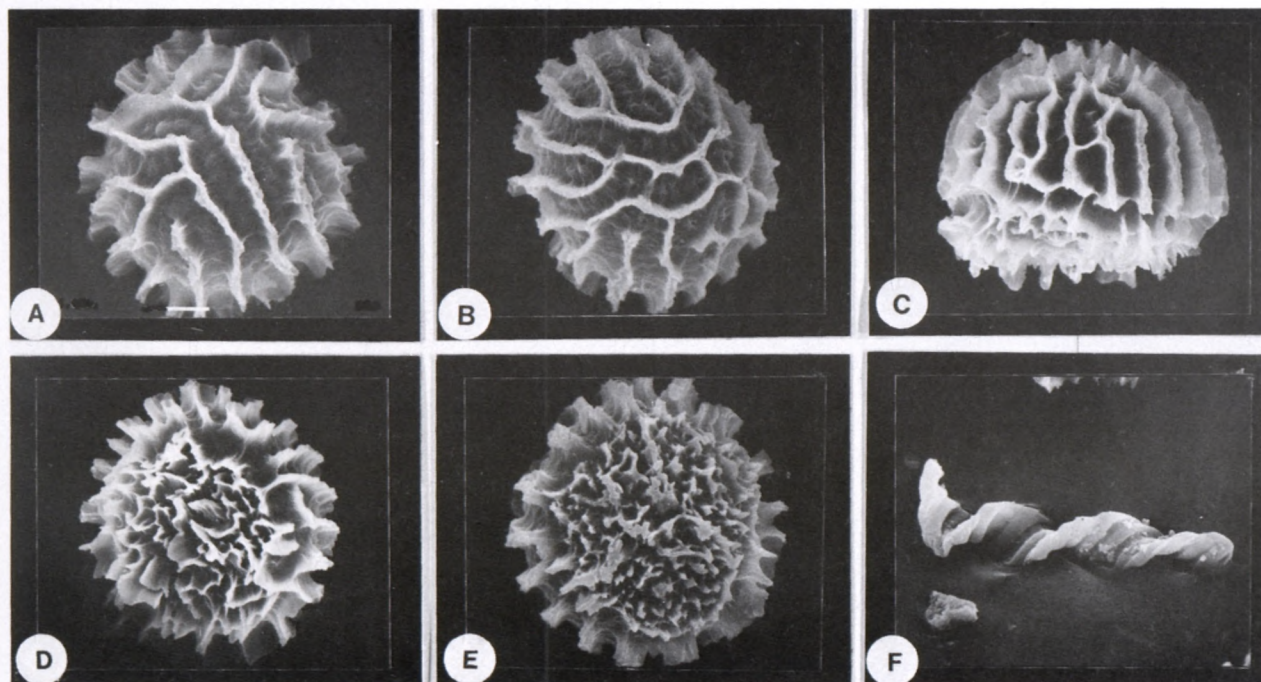


FIGURE 3.—*Fossombronia gemmifera*. Spores and elater. A, B, distal face; C, side view of distal face; D, E, proximal face; F, elater. A, B, D, S.M. Perold 2017; C, E, F, Strauss 132. A, $\times 734$; B, D, $\times 688$; C, E, F, $\times 535$.

Plants medium-sized, creeping, gregarious or in crowded colonies, green; shoots mostly simple, 5.0–7.0 mm long, 1.8 mm high, 3.0 mm wide, occasionally once furcate close to apex (Figure 6A) or to base (Figure 6B), moderately to widely divergent, apical segments 2–5 mm long. *Stems* prostrate, fleshy, in cross section at apex 400–500 μm (13 cell rows) high, 530–650 μm wide, tapering proximally, at base (300–) 400–450 \times 400–480 μm , plano-convex (Figure 5I). *Rhizoids* purple, 12–20 μm wide. *Leaves* overlapping, undulating, very obliquely inserted succubously, generally oblong, longer than wide and wider above than basally, 2000–2500 μm long, width 1325–2500 μm above, 1050–1400 μm below, apex subtruncate, with shallow angular lobes (Figure 5A–F); margins with or without 1 or 2 slime papillae, the lower one on proximal edge of leaf below midline often 2-celled (Figure 5N). *Leaf cells* thin-walled, at upper margins subquadrate, 25–30 \times 32–45 μm , at lateral margins long-rectangular, up to 87.5 \times 22.5 μm ; upper laminal cells 5- or 6-sided, 57.5–75.0 \times 27.5–37.5 μm ; middle laminal cells 62.5–102.5 \times 42.5 \times 47.5 μm ; basal cells 75.0–87.5 \times 37.5–40.0 μm . *Oil bodies* glistening, numerous, more than 50 per cell, up to 2.5 μm in diameter; chloroplasts densely scattered in cells when fresh, but later tending to clump together, $\pm 5 \mu\text{m}$ in diameter (Figure 5O).

Dioicous. *Male plants* hardly smaller than females. *Antheridia* dorsal between leaves, in a row, white when immature, later turning yellow, globose (Figure 6C), short-stalked, $\pm 210 \mu\text{m}$ in diameter, posteriorly shielded by perigonal bracts (Figure 5J–M), $\pm 550 \times 370 \mu\text{m}$, cells in interior subquadrate to hexagonal, 45.0–62.5 \times 40.0–42.5 μm , apices divided into (2)3 or 4 finger-like projections (Figure 6C), 150–300 μm long and 1 or 2 cell rows wide. *Archegonia* naked, in an interrupted, irregular row or in groups dorsally along the stem (Figure 6D). *Pseudoperianths* produced in acropetal sequence, 1 or 2 per shoot, the younger one near the apex and the other

(if present) usually more proximally, but occasionally in close proximity; sessile, \pm funnel-shaped (Figure 5H), at constricted base 425–525 μm wide, up to 1750 μm long, width across flaring mouth 2250–2375 μm , consisting of (4)5 or 6 lobes (Figure 6E), with 1–4(5) deep clefts to near the base (Figure 5G), apices truncate, entire, or with sharply pointed projections; cells comparable in shape and size to those of leaves. *Capsules* globose, $\pm 625 \mu\text{m}$ in diameter, initially entirely enveloped in calyptra, which is later shed, revealing capsule wall (Figure 6F), the latter bistratose, the inner cell layer with irregularly quadrangular cells, 32.5–37.5 \times 20.0–37.5 μm , at each cell wall 2 or 3 nodular and sometimes semi-annular thickenings, (Figure 5P). *Seta* delicate, up to 5.6 mm long, 110 μm in diameter. *Spores* brown, \pm hemispherical (Figure 7D), 40.0–52.5 μm in diameter; distal face convex, usually covered with numerous tall, conical spines up to 5 μm long (Figure 7A), rarely broken (Figure 7B), and

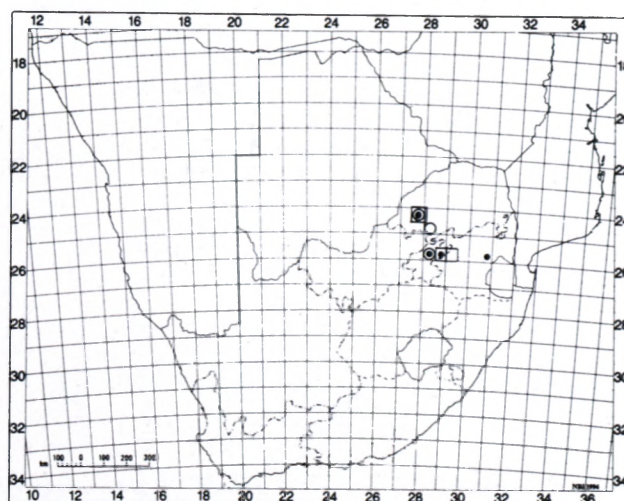


FIGURE 4.—Map showing distribution of *F. gemmifera*, \square ; *F. glenii*, \bullet ; and *F. straussiana*, \circ , in Northern Province, Gauteng and Mpumalanga.

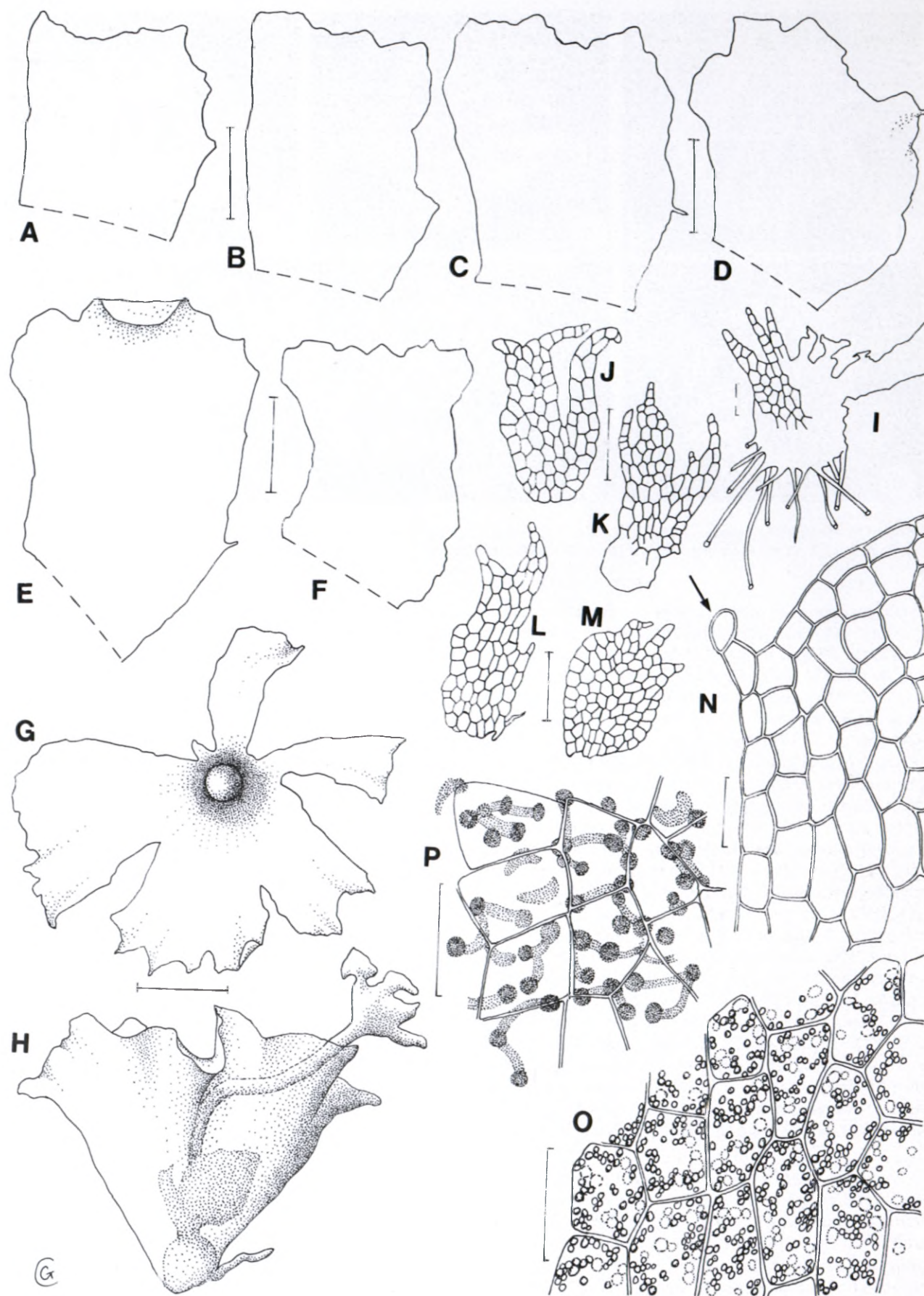


FIGURE 5.—*Fossombronina glenii*. A–F, leaves; G, opened pseudoperianth; H, pseudoperianth from side; I, stem in cross section; J–M, perigonal bracts; N, detail of marginal area of leaf, with slime papilla (see arrow); O, median leaf cells with oil bodies and chloroplasts; P, cells in capsule wall. A–C, E–K, M–P, *S.M. Perold 3052*; D, L, *Glen 2134*. Drawings by G. Condy. Scale bars: A–H, 500 μ m; J–M, 250 μ m; I, 100 μ m; N–P, 50 μ m.

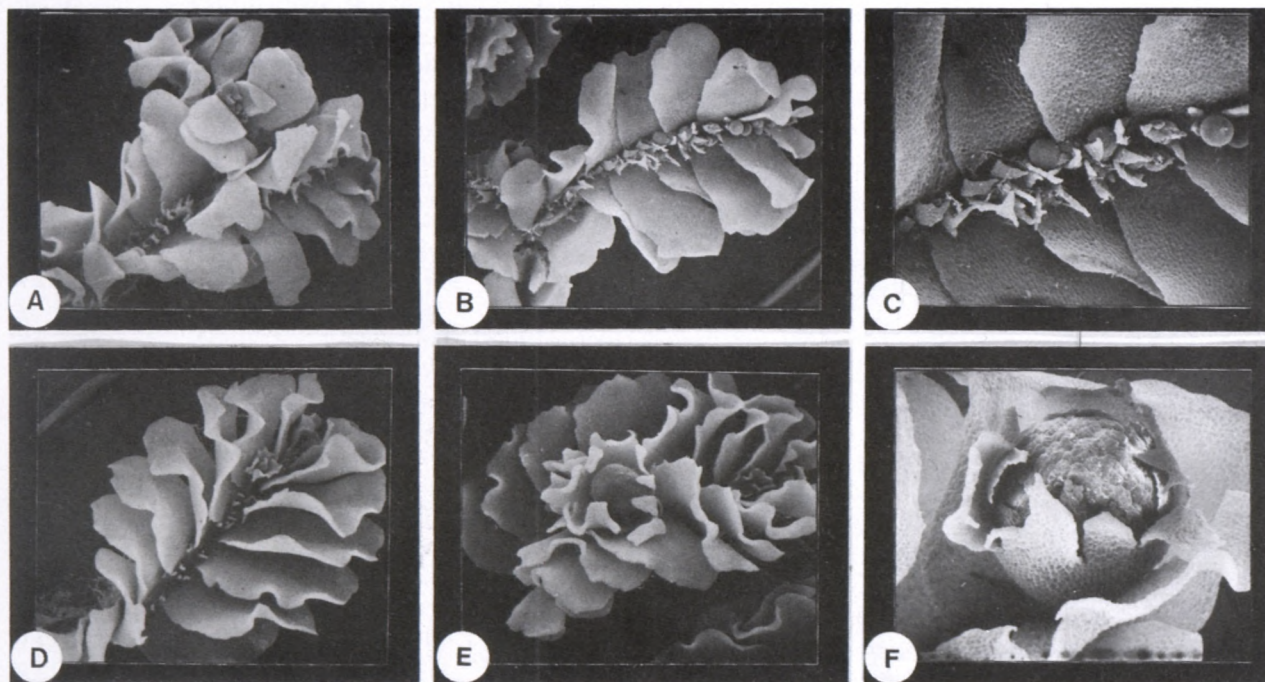


FIGURE 6.—*Fossombronia glenii*. A, stem branching near apex; B, stem branching near base; C, antheridia shielded by perigonal bracts; D, archegonia naked along stem, young pseudoperianth near apex; E, pseudoperianth with capsule from above; F, close-up of capsule in pseudoperianth. A, Perold & Van Rooy 3569; B–E, Perold & Van Rooy 3568; F, Glen 2134. A, B, D, E, $\times 7$; C, $\times 15$; F, $\times 23$.

sometimes connected by short ridges, even occasionally forming some high-walled areolae (Figure 7C); proximal face \pm flat, lacking a distinct triradiate mark, sprinkled with numerous fine to coarse tubercles (Figure 7E), which are sometimes rather flattened; circumference with numerous, up to 45, projecting spines. *Elaters* yellow, smooth, 70.0–137.5 μm long, 7.5–10.0 μm wide in middle and tapering slightly toward tips, 2- (Figure 7F) and sometimes 3-spiral in the same elater.

Fossombronia glenii grows on rather sandy soil in dry stream beds or on stream banks, or else on soil pockets in exposed rocky cliffs above streams. So far, it has only been collected at a few localities in Northern Province, Gauteng and Mpumalanga (Figure 4), but it is surely more widespread. It is easily recognized by the rather small pseudoperianth split into several lobes, by perigonal bracts with finger-like projections and by spinous spores. Because of its spinous spores, a specimen collected by Mogg (CH

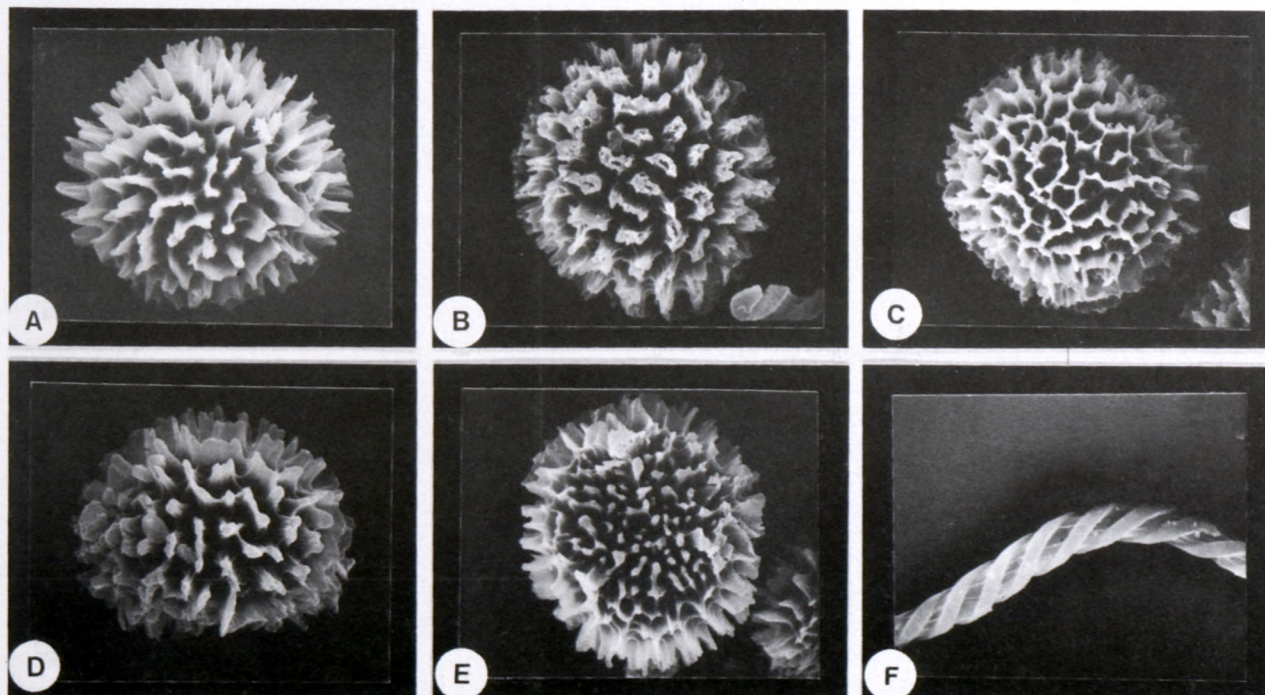


FIGURE 7.—*Fossombronia glenii*. Spores and elater. A–C, distal face; D, side view of distal face; E, proximal face; F, elater. A, F, Glen 2146; B, D, Mogg CH157; C, S.M. Perold 3052; E, Glen 2134. A, $\times 562$; B, $\times 700$; C, $\times 737$; D, $\times 694$; E, $\times 582$; F, $\times 575$.

157) at Wonderboom Poort, Pretoria, was previously misidentified as the so-called *F. crispa*, but the name had been misapplied (Perold b in press). *Fossombronia glenii* is distinguished from the winter rainfall species, *F. leucoxantha*, by the dentate leaves and pseudoperianths (Perold a in press). Both species have spinous spores.

This species is named in honour of an esteemed colleague at the National Botanical Institute, Dr H.F. Glen, who has often collected liverworts, together with his wife, Mrs R. Glen (another colleague) and their young daughter, Melissa.

3. *Fossombronia straussiana* Perold, sp. nov.

Plantae repentes, crebrae in coloniis. *Folia* plerumque valde convoluta, dense imbricata, irregulariter formata, longiora vel breviora quam latiora, interdum cum appendiculo oblongo in basi proximali. *Rhizoidea* hyalina vel brunnescentia. Monoicae. *Antheridia* archegoniae conferta, appendiculo foliari basali partialiter circumdata. *Pseudoperianthium* campanulatum, orificio patenti lobati, processibus plures lamellatis lateraliter procurrentibus. *Sporae* 35.0–42.5 µm diametro distaliter usque ad 10 lamellis discontinuis, cristis tenuibus interjunctis, aliquando areolas imperfectas facientibus, saepe inclusionibus papilliformibus vel cruciformibus; superficie proximali cum nota triradiata imperfecta, non valde distincta, superficiebus cum papillis humilibus et cristis irregularibus brevibus tectis. *Elaters* 107.5–175.0 µm longi, ter vel bis spirales, papillis tenuibus humilibus tecti.

TYPE.—Northern Province, 2427 (Thabazimbi): Kransberg, Farm Geelhoutbosch, on streambank, directly south of rondavel, (–BC), *S. Strauss* 133 (PRE, holo.); *S. Strauss* 134, same locality (PRE, para.).

Plants medium-sized, creeping, in crowded colonies, green; shoots simple, up to 9.5 mm long, 1.4 mm high, 2.3–3.0 mm wide, or once-furcate, apical segments narrowly divergent (Figure 9A), 4.5–7.5 mm long, basal part 3.0–4.5 mm long. *Stems* prostrate, fleshy, in cross section at apex (300–)400–500 µm (13 cell rows) high, 550–680 µm wide, tapering basally to 300 × 320 µm, plano-convex (Figure 8K). *Rhizoids* of all plants entirely hyaline or brownish, 10.0–12.5 µm wide. *Leaves* mostly highly convoluted, densely imbricate (Figure 9B), obliquely inserted succubously, irregularly shaped, longer than wide (Figure 8B, C) to shorter than wide (Figure 8A, E, F), (575–) 1300–1500 × (850–)1025–1500 µm, sometimes with an oblong appendage at proximal base (Figure 8C, D), ± 675 × 500 µm; margins with up to 8 slime papillae at angulations or in between, 22.5–27.5 × 22.5–25.0 µm. *Leaf cells* thin-walled, at upper margins subquadrate or rectangular across (Figure 8L), 25.0–27.5 × 30.0–40.0 µm; at lower lateral margins long-rectangular, up to 47.5 × 22.5 µm; upper laminal cells subquadrate, 25.0–32.5 × 30.0–32.5 µm; middle laminal cells 5- or 6-sided, 47.5–62.5 × 27.5–40.0 µm; basal cells 70.0–75.0 × 50.0 µm. *Oil bodies* glistening, faintly granular, 10–25 per cell, up to 2.5 µm in diameter; chloroplasts densely scattered in cells, 3–5 µm in diameter (Figure 8M).

Monoicous. *Antheridia* short-stalked, globose, 110–135 µm in diameter, dorsal on stem between leaves, basal leaf

appendage partly curved around 1 or 2 (Figure 9D, E), sometimes leaf appendage detached, forming an oblong perigonial bract (Figure 8J), 430–620 × 300–420 µm, margin with 1 or 2 papillae. *Archegonia* in close proximity to antheridia. *Pseudoperianths* soon forming (Figure 9C) after fertilization in acropetal sequence, often 2 per shoot, close together near apex, older more proximal one sometimes with capsule already dehiscent; sessile, campanulate (Figure 9F), at constricted base ± 600 µm wide, 1250 µm, rarely to 1825 µm long, width across flaring mouth 2250 µm, margin ± scalloped, consisting of 4–7 shallow, rounded lobes (Figure 8H), several lamellate outgrowths projecting laterally from sides (Figure 8I); cells comparable in shape and size to those of leaves. *Capsules* globose, 500–610 µm in diameter, capsule wall bistratose, cells in inner layer irregularly shaped, 30.0–37.5 × 15.0–20.0 µm, crowded with nodular and some semi-annular thickenings (Figure 8N). *Seta* 2.25–4.0 mm long, 140–150 µm in diameter, 6 or 7 cells across (Figure 8G). *Spores* light brown, hemispherical (Figure 10B), 35.0–42.5 µm in diameter, including marginally projecting lamellae; distal face convex (Figure 10A, C, D), ornamented with up to 10 discontinuous lamellae, ± 2.5 µm long and 5.0–7.5 µm apart, but interconnected with faint cross ridges, sometimes forming incomplete areolae and frequently with papilla-like or cross-like inclusions; proximal face (Figure 10E) with incomplete and not very distinct triradiate mark, facets covered with low papillae and short irregular ridges, up to 25 lamellae projecting around periphery. *Elaters* light brown, 107.5–175.0 µm long, 7.5 µm wide in middle, tapering to ends, 3-spiral or partly 2-spiral, covered with fine, low papillae (Figure 10F).

Fossombronia straussiana is often mixed with other *Fossombronia* species and grows on streambanks and in seepage areas at several localities in the Northern Province and Gauteng (Figure 4). More specimens of it, *J. Braggins* 91/191 and *S.M. Perold* 2654, were collected in 1991 in Malawi on the Zomba Plateau, as well as at Nyika Nat. Park, *S.M. Perold* 2663; thus it appears to be widespread. Vanden Berghen (1965) reported *F. husnotii* (with hyaline rhizoids) from the Congo Republic, *Symoens* 4329, and from Tanzania (= Tanganyika), *Bryan* 1036. The spores of these specimens have much taller lamellae than those of *F. straussiana* and also appear to differ from those of *F. husnotii*. In 1978 Vanden Berghen reported *F. husnotii* from Shaba, Zaïre (*Malaisse* 9039), without mentioning the rhizoids, but presumably referred here because they are hyaline. Scott & Pike (1988a) comment that the spores of *F. husnotii* are extraordinarily variable and that more research is required. Beside *F. husnotii*, which has mostly hyaline rhizoids, Scott & Pike (1984) also described three new Australian species, *F. punctata*, *F. scrobiculata* and *F. vermiculata*, as having hyaline rhizoids on all or on most plants.

Fossombronia straussiana has been named in honour of Mrs Susan Strauss, owner of the Farm Geelhoutbosch, where she has collected it a number of times, together with other *Fossombronia* species.

This species is easily distinguished by its hyaline or brownish rhizoids and dense, frilly leaves, its pseudoperianth with lamellate, lateral outgrowths, by the spore ornamentation that usually has incomplete areolae with

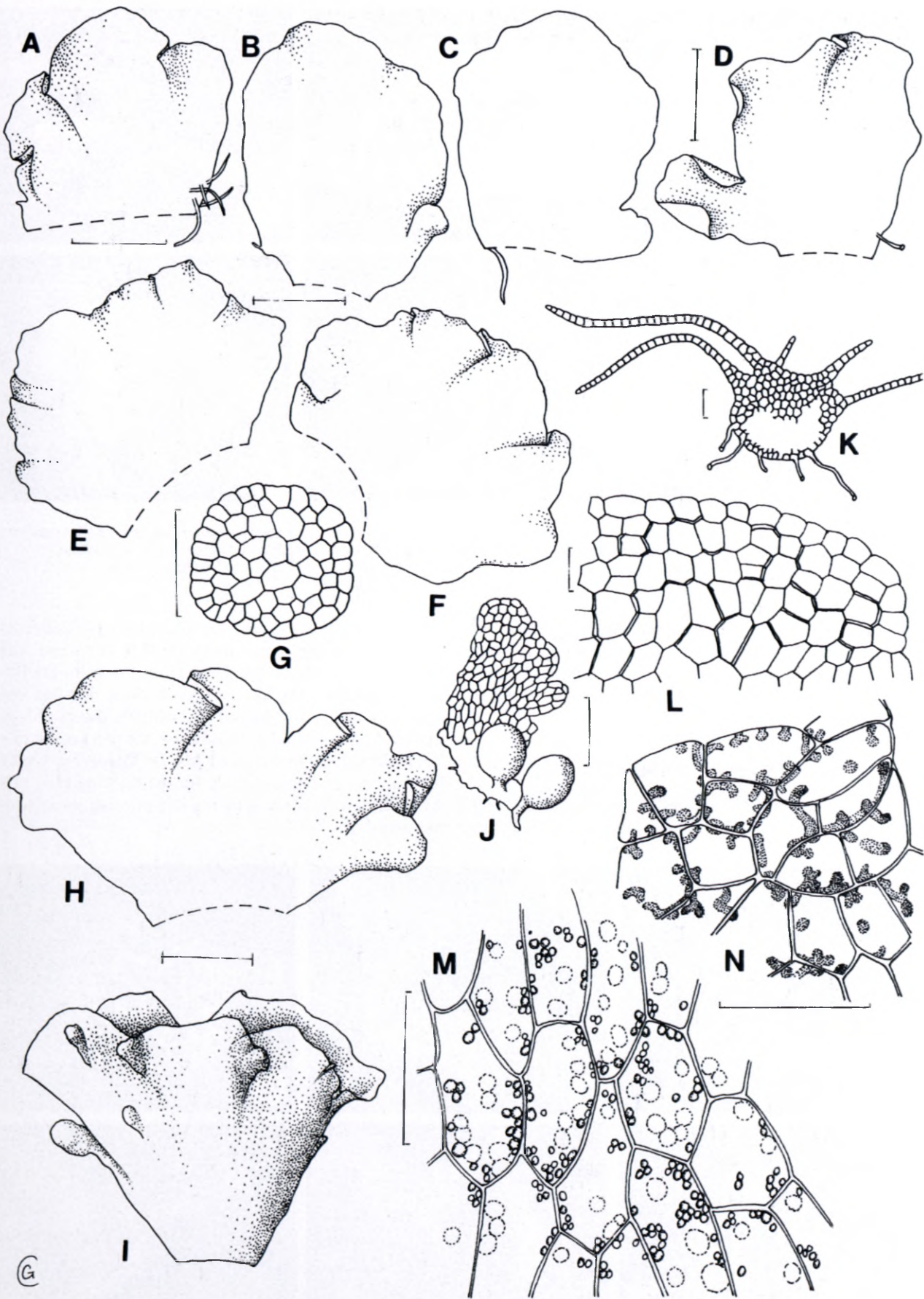


FIGURE 8.—*Fossombronina straussiana*. A–F, leaves; G, cross section of seta; H, opened pseudoperianth; I, pseudoperianth from side; J, perigonial bract and 2 antheridia; K, cross section of stem; L, detail of leaf margin; M, median leaf cells with oil bodies and chloroplasts; N, cells in capsule wall. A–C, E, F, H, I, K, N, *Strauss & Retief CH13655*; D, J, *Perold & Koekemoer 3116a*; G, *Strauss CH13653*; L, M, *Strauss CH13651*. Drawings by G. Condry. Scale bars: A–F, H, I, K, N, 500 µm; G, K, 100 µm; J, 250 µm; L–N, 50 µm.

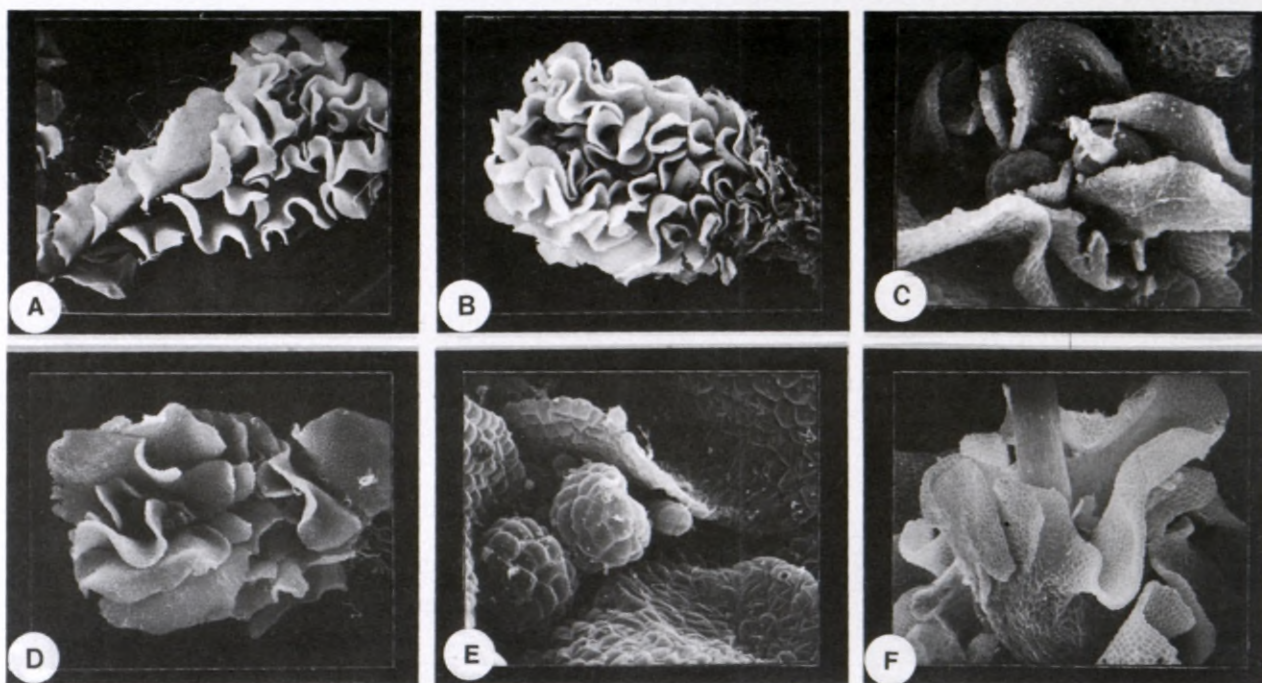


FIGURE 9.—*Fossombronina straussiana*. A, stem branching near apex; B, leaves crowded on stem; C, antheridium and archegonium in close proximity between leaves; D, proximal leaf appendage curved around gametangia; E, close-up of same; F, pseudoperianth with seta emerging from it. A, F, Strauss 133; B, Perold & Koekemoer 3124a; C–E, Perold & Koekemoer 3116a. A, $\times 7$; B, $\times 10$; C, $\times 66$; D, $\times 15$; E, $\times 106$; F, $\times 23$.

inclusions and by the usually finely papillose elaters. The specimen, *Scott 13*, has a larger and more elaborate pseudoperianth than those usually encountered in this species. Its spore ornamentation is very similar, however, and the rhizoids are hyaline.

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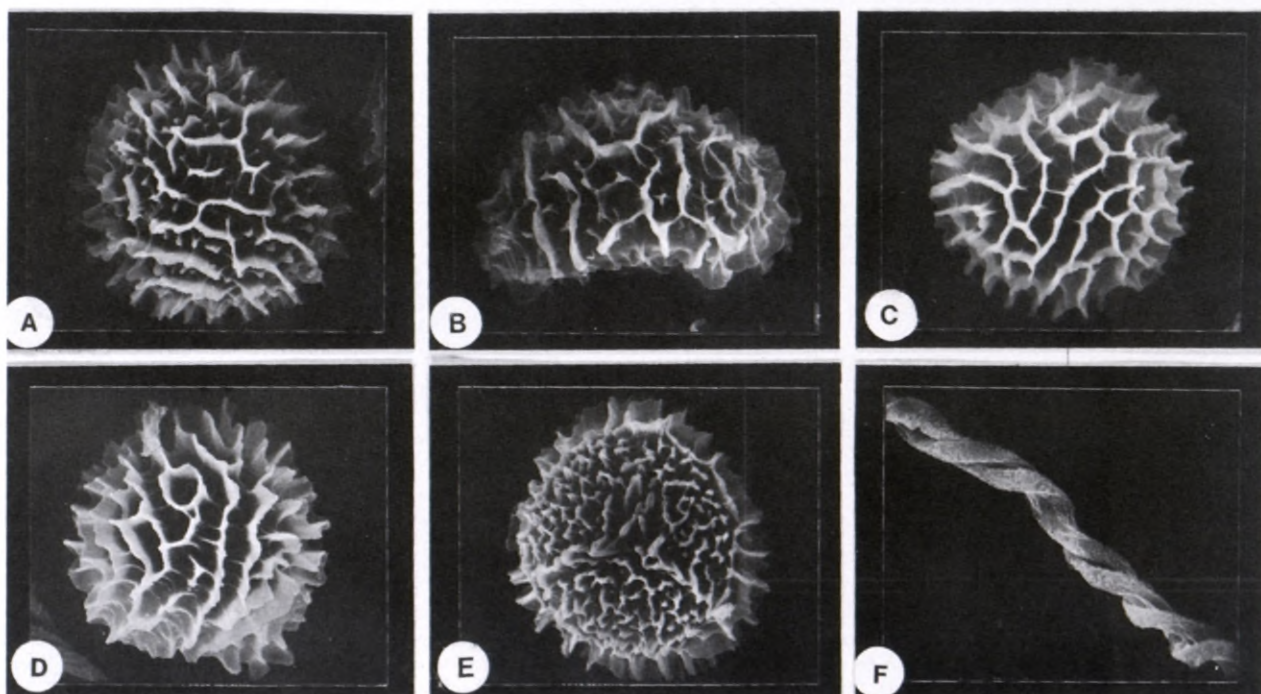


FIGURE 10.—*Fossombronina straussiana*. Spores and elater. A, C, D, distal face; B, side view of distal face; E, proximal face; F, elater. A, B, E, *Scott 13*; C, Strauss & Retief CH13655; D, S.M. Perold 3280; F, Perold & Koekemoer 3124a. A, C, $\times 727$; B, $\times 1084$; D, $\times 588$; E, $\times 674$; F, $\times 839$.

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SPECIMENS EXAMINED

Held at PRE, unless otherwise indicated. Bracketed numbers after citation of collector's name and collecting number refer to the species described in the text in alphabetical order, namely: *F. gemmifera* (1); *F. glenii* (2); and *F. straussiana* (3).

Braggins 91/191 (3) (Malawi).

Glen 2134 (2) (paratype), 2146 (2) (holotype).

Koekemoer 976 (2).

Mogg CH157 (2) BOL, PRE.

Perold S.M. 2017 (1); 3052 (2); 3280, 3281, 2654 (Malawi), 2663 (Malawi) (3). Perold & Koekemoer 3116a, 3124a (3); 3116b, 3124b, 3129 (1). Perold & Van Rooy 3555, 3559a (paratype), 3564, 3565 (1); 3568, 3569 (2).

Scott 13 (3) CH3697. Strauss 132 (1) (holotype), 133 (3) (holotype), 134 (3) (paratype), CH13651, CH13653, CH13654 (3). Strauss & Retief CH13655 (3).

Wager 14 (3).