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Studies in the liverwort genus *Fossombronia* (Metzgeriales) from southern Africa. 4. A re-examination of *F. crispa*, *F. leucoxantha* and *F. tumida*

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Keywords: *Fossombronia*, *F. crispa*, *F. leucoxantha*, *F. tumida*, Hepaticae, Metzgeriales, southern Africa

ABSTRACT

The above three southern African species were described during the nineteenth century, but the descriptions are brief and mostly inadequate. The practice, albeit for justified financial reasons, of dividing collections (which were often mixed) and of distributing the parts to different herbaria, has led to some later authors applying the specific epithets to the wrong components. This has caused a great deal of confusion, and much time and effort have been expended in sorting out these misapplications. This paper aims to correct and to report on some past mistakes. Detailed descriptions, illustrations and a distribution map of these three species are accordingly provided.

1. **Fossombronia crispa** *Nees* in Synopsis Hepaticarum, Gottsche et al.: 469 (1846). Type: Cap. de b. Spei, leg. presumably *Zeyher*, no collector's name on label, only the number 3, probably added later (STR, lecto.! fide Perold 1997d).

Jungermannia crispa Sprengel in schedule Herb. Zeyher.

J. pusilla Lehm. : 369 no. 42, *Ecklon* (BM!).

Fossombronia zeyheri Steph.: 32 (1900); Sim: 35 (1926); S.W. Arnell: 79 (1963); Sérgio: 191 (1985). Type.—Cap. b. spei, leg. *Zeyher s.n. G024669*(G!) ex Herb. Rabenhorst, idem ex Herb. (?)*ope, G024670*(G!), portion(s) of type, sub *F. crispa*.

Plants in dense colonies, pale green or bright green to glaucous green; medium-sized to robust; shoots simple, (8–)12–15 mm long, 1.5–2.0 mm high, 3.2–3.4 mm wide, or once/twice or repeatedly furcate, terminal segments moderately divergent, 3.0–5.0 mm long. *Stems* prostrate, chlorophyllose, sometimes outer cells purple, occasionally with a lateral bud, later developing into a side shoot, plano-convex in cross section, apically frequently swollen, 320–350 µm (13 cell rows) high, 500–540 µm wide (Figure 1G), tapering proximally and toward base (Figure 1H), 220–230 µm high, 270–300 µm wide. *Rhizoids* purple, 12.5–22.5 µm wide. *Leaves* (Figure 1A–F) overlapping, widely spreading to suberect (Figure 2A), slightly undulate to crispate, succubously inserted, apically small, soon enlarging, oblong to irregularly rectangular, somewhat longer than wide or occasionally as long as wide or even shorter than wide; 1450–1950 × 1250–2000 µm, often narrower below, 750–1375 µm; apex rounded or truncate, sometimes 2 or 3 times slightly notched and shallowly lobed, margins (Figure 1I) entire, but with 7–14 unicellular slime papillae, generally well spaced, but at proximal (trailing) edge closer together and occasionally raised on a basal cell. *Leaf cells* thin-walled, at upper margins mostly rectangular across, 10.0–37.5 × 42.5–75.0 µm, at lateral margins long-rectangular, 67.5–80.0 × 15.0–22.5 µm, upper laminal cells 5- or 6-sided, 50.0–57.5 × 37.5–52.5 µm, middle laminal cells 87.5–107.5 × 35.0–45.0 µm, basal cells 120.0–137.5 × 30.0–47.5 µm. *Oil bodies* variable in number, 9–45 per cell, round, smooth or granular, up to 5 µm in diameter (Figure 1J); chloroplasts numerous, crowded, ± 5 µm in diameter (Figure 1J).

Monoicous (Figure 2B, C), sometimes seemingly dioicous. *Antheridia* short-stalked, globose, dorsal on stem, sometimes crowded together near apex of shoot, interspersed with the younger archegonia and apparently naked (Figure 2B), at other times proximal to pseudoperianth (or on different plants) and subtended by perigonial bracts (Figure 2D), their shape irregular (Figure 1K–N), 400–850 × 250–450 µm wide across broadest part, mostly narrower toward apex and base, margins with up to 7 papillae or with 1 or 2 short, finger-like processes, cells in interior 5- or 6-sided, 112.5–117.5 × 30.0–42.5 µm, marginally 32.5– 50.0 × 20.0–50.0 µm. *Archegonia* in 1 or 2 irregular rows along stem, even extending toward base (Figure 2A), naked, sometimes 2 in close proximity becoming fertilized (Figure 2E). *Pseudoperianth* campanulate (Figure 1O, P), at apex of branch or close to it, as tall as, or up to 375 µm taller than leaves, raised on a short stalk, 375–500 µm long, 550–600 µm wide, then widely flaring upwards, 1625–2150 µm long, 2500–2925 µm wide across mouth, margin with ± 5 main undulating lobes (Figure 2F), generally subdivided into smaller ones, at side mostly cleft once to base, often with lamellar outgrowths, 1125–1375 × 375 µm; cells not appreciably different from those of leaves. *Capsules* globose, ± 550 µm in diameter, wall bistratose, cells of inner layer irregularly shaped, 25.0–75.0 × 20.0–35.0 µm, each cell wall with 3 or 4 dark brown nodular and occasionally semi-annular thickenings (Figure 1R). *Seta* 2.9–4.4 mm long, ± 150 µm in diameter, ± 7 cell rows across (Figure 1Q). *Spores* light brown, 37.5–42.5 µm in diameter, including lamel-

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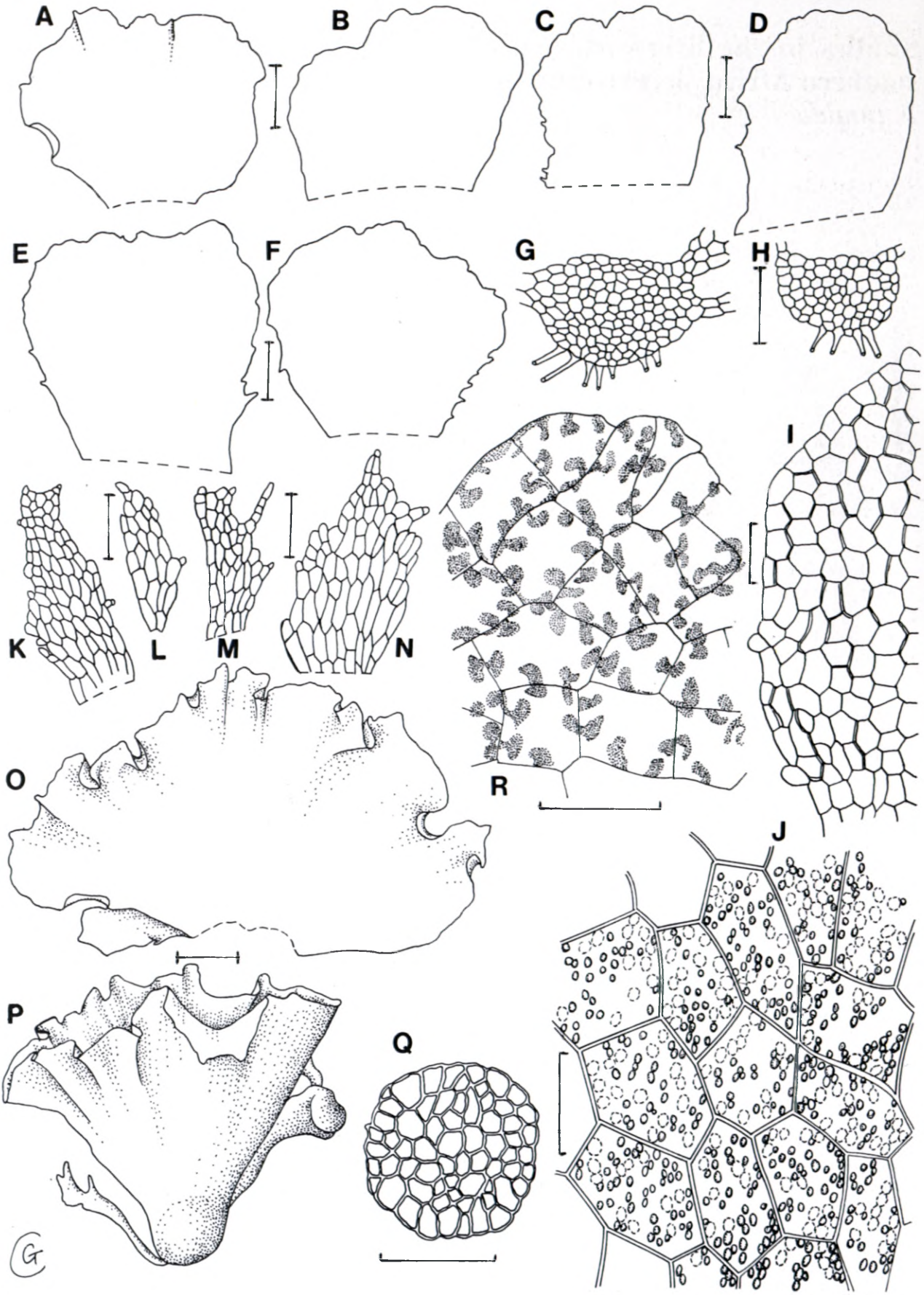

FIGURE 1.—*Fossombronia crispa*; A–F, leaves; G, cross section of stem apex; H, cross section of stem base; I, detail of leaf margin; J, median leaf cells with oil bodies (solid lines) and chloroplasts (dotted lines); K–N, bracts; O, opened pseudoperianth; P, pseudoperianth from side; Q, cross section of seta; R, cells in capsule wall. A, C–F, K–P, *S. Strauss 134a*; B, I, J, *S. Strauss CH13664*; G, H, R, *Perold & Van Rooy 3558*; Q, *J. Victor 1379*. Scale bars: A–F, O, P, 500 µm; G, H, K–N, 250 µm; I, J, R, 50 µm; Q, 100 µm. Artist: G. Condy.

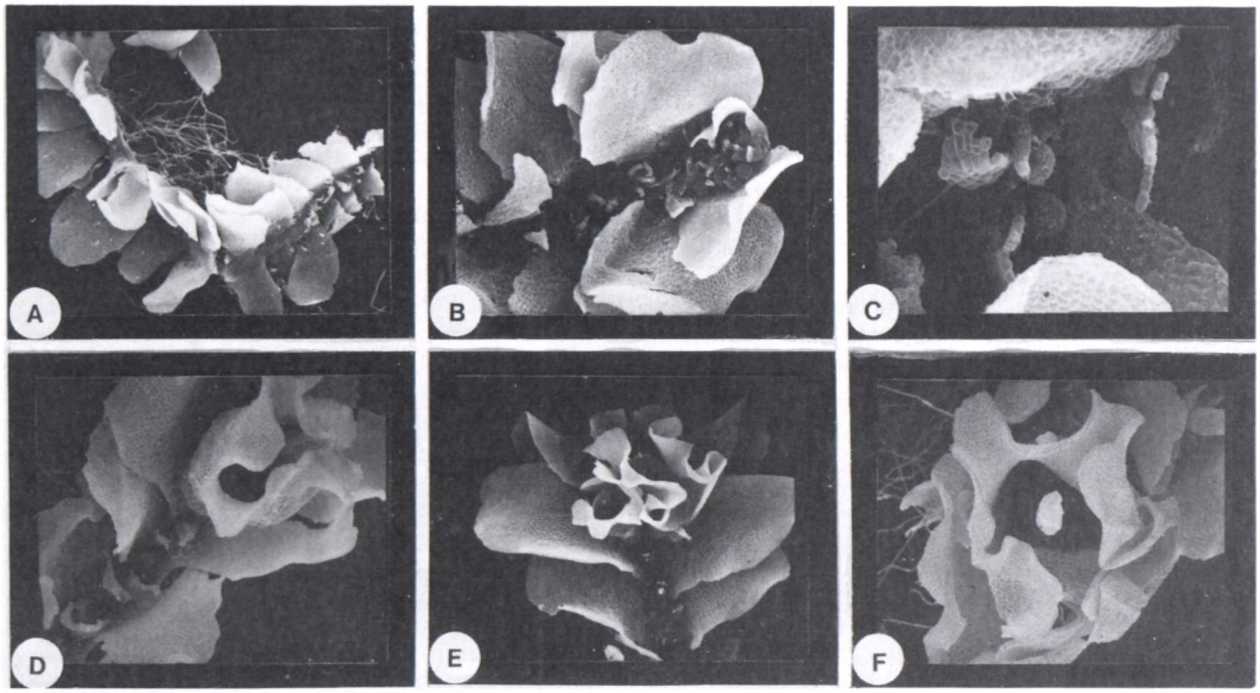

FIGURE 2.—*Fossombronia crispa*. A, simple stem, leaves widely spreading; B, apex of segment with crowded antheridia and archegonia, more distally; C, apex of stem with naked antheridia, archegonia and a bract; D, pseudoperianth near apex of stem and bracts more proximally; E, two adjacent pseudoperianths; F, pseudoperianth from above. A, E, *S.M. Perold 3444*; B, *Perold & Koekemoer 3282*; C, *S.M. Perold 3280* p.p.; D, F, *S. Strauss 134a*. A, × 7; B, × 13; C, × 41; D, × 15; E, × 8; F, × 19.

lae projecting around periphery; hemispherical; distal face (Figure 3A, B) convex, ornamentation over polar area reticulate or partly reticulate, low, slightly wavy lamellae forming ± 6 complete and incomplete, irregular areolae across diameter of face (a total of 15–24), each 7.5–12.5 µm wide, sides of lamellae with a few faint buttressing striations that soon disappear, spore surface between lamellae granular (Figure 3C); proximal face lacking triradiate mark, flat, covered with fine, low ridges forming very small, irregular areolae, with papillae here and there (Figure 3D), otherwise very coarsely granular, toward centre of face granules coalescing into large, irregular clumps (Figure 3E), around spore periphery 14–18 low 'spines', which are the 'ends' of the lamellae from the distal face extending over the sides and are connected by a low, much interrupted, membranous wing or perispore. *Elaters* (Figure 3F) yellow-brown, 60.0–122.5 µm long, 7.5–12.5 µm wide in cen-

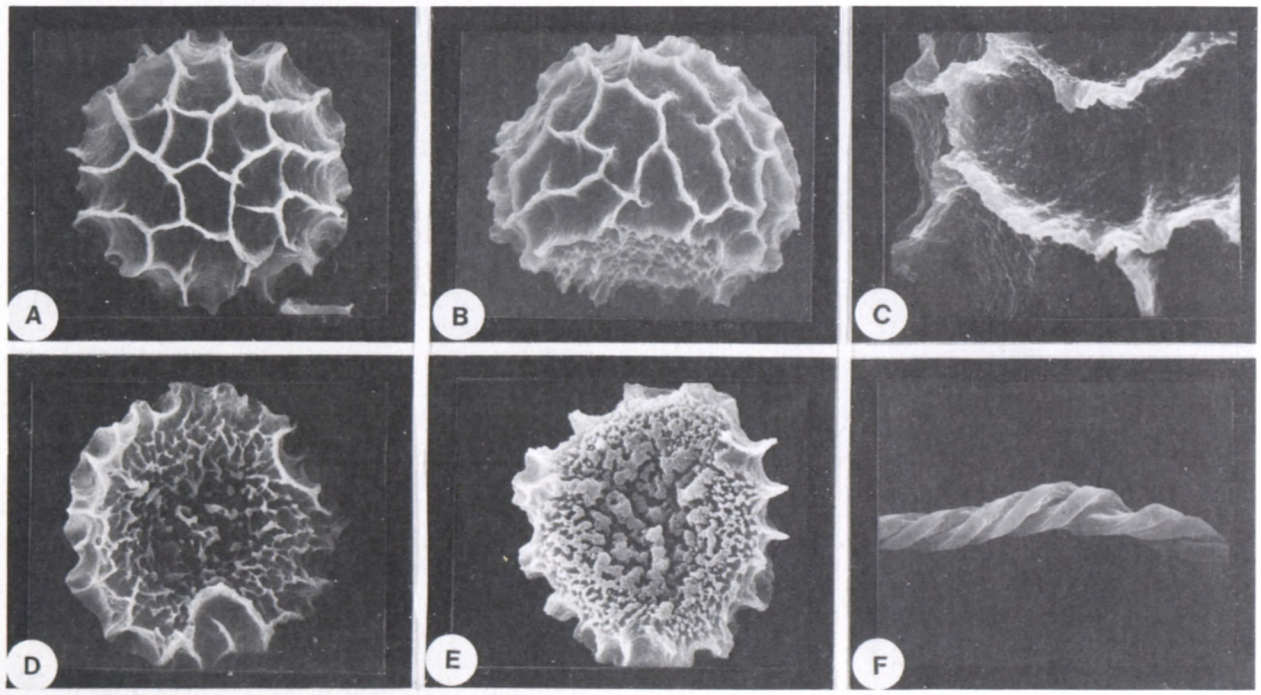

FIGURE 3.—*Fossombronia crispa*. A–E, spores: A, distal face; B, side view of distal face; C, detail of lamellae and surface on distal face; D, E, proximal face. F, elater. A, D, *S.M. Perold 3317*; B, *S.M. Perold 3280* p.p.; C, *S.W. Arnell 2201*; E, *S.M. Perold 3444*; F, *Perold & Van Rooy 3558*. A, × 725; B, × 859; C, × 2596; D, × 705; E, × 685; F, × 852.

tre, tapering to one or both tips and ending in a 5 µm wide loop, or not tapering, ends blunt, with 2 or 3 loose spirals or tightly coiled.

Fossombronia crispa grows on soil at river banks, seepage areas and at road sides. Although fairly frequently sterile, it is, nevertheless, the most common southern African species of *Fossombronia* and its range extends from the winter rainfall area of Western Cape to the summer rainfall areas of Eastern Cape, KwaZulu-Natal, Mpumalanga and Northern Province (Figure 4). When fertile, the species bears ripe sporangia during most of the year in the summer rainfall areas. Since *F. crispa* is so common, it is clear why it was first described by the mid 1800's and not as late as 1900 by Stephani under the epithet, *F. zeyheri*.

Fossombronia crispa is distinguished by its entire, crisped leaves, its frequently robust size, generally purple stem, pseudoperianths with lobed, undulating mouth, reticulate or incompletely reticulate spores with low lamellae and elaters with strong spirals. Although there is some similarity in their spores, the elaters of *F. crispa* are clearly different from those of typical *F. capensis* (see Perold 1997b), which are short, have weak spirals and collapse upon drying.

It is shown in Perold (1997d) that *F. crispa* Nees, as described in the protologue, definitely has entire leaves. The spores, as was later found, are reticulate or incompletely reticulate but certainly not spinose. This species was subsequently redescribed by Stephani (1900) as *F. zeyheri* (sub *F. crispa*), and was considered by Scott & Pike (1987a) to be part of the widely distributed and later described, *F. foveolata* complex, because of similarities in spore ornamentation. By inference *F. crispa* would also be part of this complex. It was, however, described 30 years before *F. foveolata* and the specific name, *F. crispa*, would therefore have priority. In general, *F. crispa* is a larger plant than *F. foveolata* and I continue to treat them as distinct taxa, because this study is as yet confined to southern African species. Moreover, the specific epithet, *F. foveolata*, has a long history of acceptance.

The epithet, *F. crispa*, has, however, since Stephani (1900) generally been misapplied to plants with dentate leaves and spinose spores (i.e. *F. leucoxantha*). For some reason Scott & Pike (1988) regarded the BM specimen, (top right corner of herbarium sheet, Perold 1997d: fig. 6C), as the type of *F. crispa*. They referred to it as 'Cape of Good Hope, leg. *Zeyher*, sub '*Jungermannia crispa*' Sprengel, BM (hb. Hampe. sin. num. 14/8/1825)' and annotated it on the sheet as 1:3. As I learnt from the label, this specimen is most likely an *Ecklon* collection, no. *64*, and was gathered on Devil's Peak (Teufelsberg). I consider it to be a possible syntype of *F. leucoxantha* (Perold 1997d).

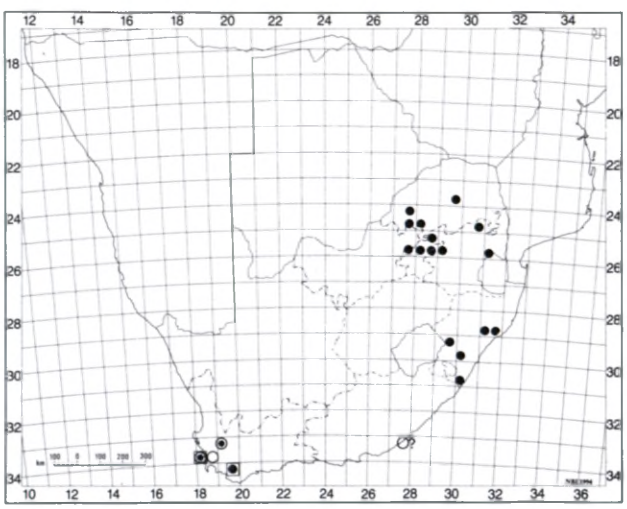

FIGURE 4.—Distribution of *F. crispa*, ●; *F. leucoxantha*, □; and *F. tumida*, ○, in southern Africa.

2. **Fossombronia leucoxantha** *Lehm.* in Linnaea 4: 368 (1829); Lehm.: 55 (1831); Sim: 36 (1926). Type: Cape of Good Hope, Table Mountain, *Ecklon* sub *Jungermannia leucoxantha* n.sp., cf. Hepat. Capens. L. 29 (S, lecto.!, fide Scott & Pike 1987b) (BM, isolecto.!; the identity of the duplicate in BM was confirmed with the aid of spores found in the glue on the sheet).

Plants in scattered loose colonies or in crowded patches, young apical leaves bright green, small, older leaves larger, soon becoming pale yellow or tinged with pink and translucent, medium-sized; shoots smaller in male plants, 6.0 mm long, 0.8 mm high, 1.5 mm wide; female plants larger, simple, up to 7.5 mm long, 2.6 mm high, 1.0 mm wide apically, increasing to 4.0 mm wide more proximally, sometimes once (Figure 6A), rarely twice furcate, terminal segments moderately divergent, only ± 1.5 mm long. *Stems* prostrate, green, outer cell layer becoming red, planoconvex in cross section, in male plants apically 175–300 µm (11 cell rows) high, 400–550 µm wide, in female plants apically (Figure 5K) ± 375 µm (11 or 12 cell rows) high, 600–750 µm wide, tapering proximally (Figure 5L), 230 µm high, 400 µm wide. *Rhizoids* purple, 12.5–22.5 µm wide, some with internal mycorrhizal hyphae and broad, flat tips. *Leaves* suberect to partly spreading, overlapping, mostly 'ruched' above, succubously inserted on stem, often decurrent, shape irregular, sometimes like a half-opened fan, shorter than wide or as long as wide or almost as long as wide above, generally narrower toward base, apex somewhat irregularly rounded to nearly truncate, margins with few to several folds (Figure 6B) and 7–24(–30) toothed projections, (more numerous on the proximal (trailing) edge), 1–3 (4) cells high, topped with a slime papilla; in male plants leaves (Figure 5A–E) smaller, 500–1300(–1675) × 425–875(–1375) µm; in female plants (Figure 5F–H) larger, 1575–2250 µm long, width above 1875–3950 µm and below 550–1500 µm. *Leaf cells* mostly thin-walled, in male plants generally somewhat smaller but otherwise not appreciably different from females, at upper margins (Figure 5I) subquadrate to rectangular across, 32.5–42.5 × 27.5–55.0 µm, at lower lateral margins long-rectangular, 50.0–87.5 × 17.5–40.0 µm, upper laminal cells 5- or 6-sided, 50.0–67.5 × 40.0–62.5 µm, middle laminal cells 75.0–112.5 × 37.5–65.0 µm; basal cells 100.0–162.5 × 37.5–50.0 µm. *Oil bodies* 14–18 per cell, tiny; chloroplasts in young apical leaves numerous, granular, round or oval, 5 µm in diameter (Figure 5J).

Dioicous. *Antheridia* dorsal on stem, usually in 2 crowded rows (Figure 6C, D), short-stalked, globose, 320–380 µm in diameter, turning yellow, each subtended by a perigonial bract (Figure 5M–O), sometimes

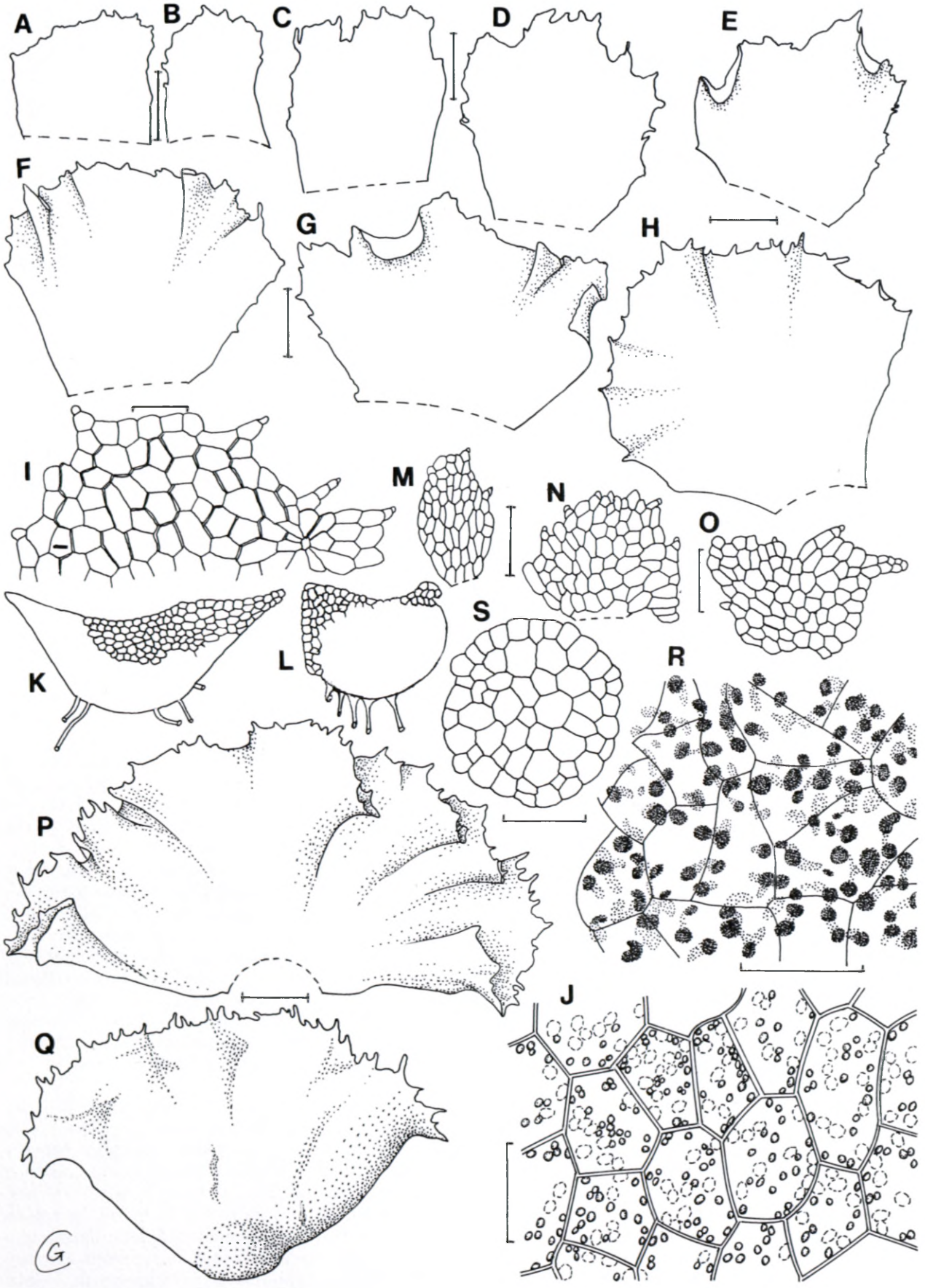

FIGURE 5.—*Fossombronia leucoxantha*. A–E, male leaves; F–H, female leaves; I, leaf margin; J, median leaf cells with oil bodies (solid lines) and chloroplasts (dotted lines); K, cross section of female stem apex; L, cross section of female stem base; M–O, bracts; P, opened pseudoperianth; Q, pseudoperianth from side; R, cells in capsule wall; S, cross section of seta. A, B, F, G, I, K, M–Q, *Oliver 9225*; C–E, H, J, L, S, *S.M. Perold 3340*; R, *S.M. Perold 3329*. Scale bars: A–H, P, Q, 500 µm; K–O, 250 µm; I, J, R, 50 µm; S, 100 µm. Artist: G. Condy.

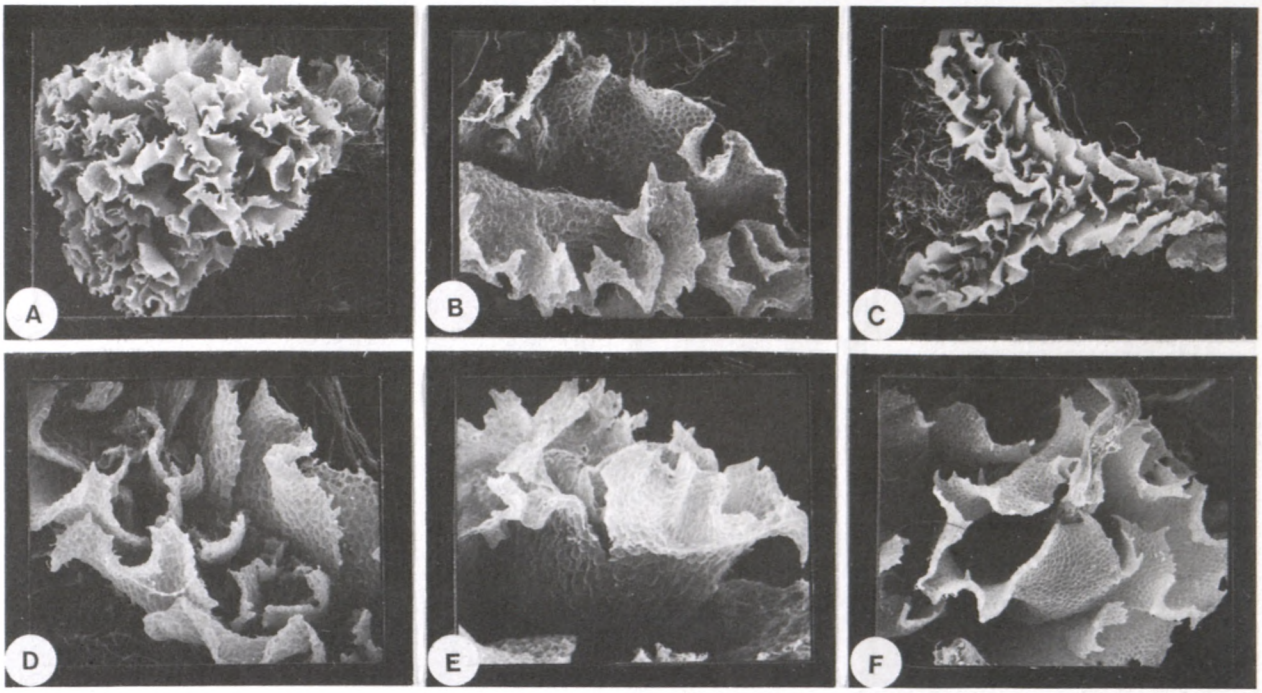

FIGURE 6.—*Fossombronia leucoxantha*. A, branched female stem; B, detail of leaves; C, branched male stem; D, detail of bracts; E, pseudoperianth from side; F, pseudoperianth from above. A–E, *Oliver 9225*; F, *S.M. Perold 3340*. A, × 8.3; B, × 21.6; C, × 8; D, × 25; E, × 24; F, × 17.

coloured pink, 310–450 × 200–400 µm, occasionally 2 adjacent ones joined together, margins with 3–5 papillae, cells of interior 4–6-sided, 50.0–75.0 × 30.0–37.5 µm. *Archegonia* in 1 or 2 rows along stem, hidden by leaves, sometimes 2 in close proximity becoming fertilized. *Pseudoperianth* (Figure 6E, F) campanulate, proximal to apex, as tall as leaves or projecting somewhat above them, raised on a short stalk, then widely flaring above, 1500–2250 µm long, 750–1500 µm wide at base, 2375–4375 µm wide across mouth, margin much 'ruched', with several 'folds' and up to 39 toothed processes (Figure 5P, Q), 3–7 cells or 100–325 µm long, topped by a slime papilla, ± 12.5 × 15.0 µm and gradually widening below; cells comparable in shape and size to those of leaves. *Capsules* globose, 800–1050 µm in diameter, wall bistratose, cells of inner layer irregularly shaped (Figure 5R), 30.0–62.5 × 32.0–50.0 µm, each cell wall with 2 or 3 dark brown, nodular, and sometimes semi-annular thickenings. *Seta* 0.2–4.0 mm long, ± 220 µm in diameter, 7 or 8 cells across (Figure 5S). *Spores* light brown, 42.5–55.0 in diameter, including spines projecting at margin (Figure 7D); hemispherical; distal face (Figure 7A–C) convex, with 12–15 truncate or conical spines up to 5 µm long, in irregular rows across diameter of spore, some confluent to form short ridges and mostly interconnected by small buttressing ridges that radiate from the bases of adjacent spines, often with several smallish papillae interspersed between spines and ridges; proximal face (Figure 7E) with triradiate mark distinct or lacking, flat, ornamentation variable, from numerous, rather fine papillae to coarse tubercles, often interspersed with short, irregular ridges, around spore periphery with up to 30 or occasionally more spines seen in profile or broadon. *Elaters* yellow-brown, 130–202 µm long, 7.5 µm wide in centre, tapering to tips, 2.5–5.0 µm wide, sometimes surface sprinkled with fine papillae (Figure 7F), bispiral or trispiral.

Fossombronia leucoxantha grows on damp, rather coarse to clayey soil at various places in the Peninsula and Western Cape, i.e. Bakoven, Bot River, Cave Peak, Chapman's Peak, Constantia Slopes, Devil's Peak, Genadendal, Karweiderskraal, Kirstenbosch Gardens, Kloofnek, between Kloofnek and Round House, Lion's Head, Round House, Signal Hill, Table Mountain and Wynberg, Cape Town (Figure 4). In this rather restricted area the species is quite common. It is distinguished by its 'ruched' leaves, of which the margins, as well as the rim of the mouth of the pseudoperianth are denticulate to incised-dentate. There are a few specimens that have almost entire leaves, notably *Esterhuysen 24885* and *Arnell 616*, that probably do not belong here in spite of having spinose spores. The spores of *F. leucoxantha* are densely spinose, but often have papillae or short ridges between the spines. This species is distinguished from *F. glenii* (Perold 1997a) which also has spinose spores, but is restricted to the summer rainfall area in Northern Province, Gauteng and Mpumalanga and its leaves are angular, and the rather small pseudoperianth is divided into deep lobes.

Fossombronia leucoxantha was described by Lehmann (1829) from an *Ecklon* collection. This *Ecklon* specimen was mixed with a tumid-leaved plant, later described by Mitten (1878) as *F. tumida* from a collection by Rev. Eaton at the Cape. Stephani's Icones (1985), nos. 3044 and 3045, illustrate *F. tumida*, but at the bottom right corner they bear the epithet, *F. leucoxantha*. In a note under his description of *F. leucoxantha*, Stephani (1900) referred to its leaves as 'aufgeblasen', which could only apply to *F. tumida*. Subsequently, Sim (1926) complained that Stephani 'mentions it [meaning *F. tumida*] near *F. leucoxantha*, which is not its place'.

Arnell (1963) placed *F. leucoxantha* Steph. (surely implying *sensu* Steph.) in synonymy under *F. tumida* and

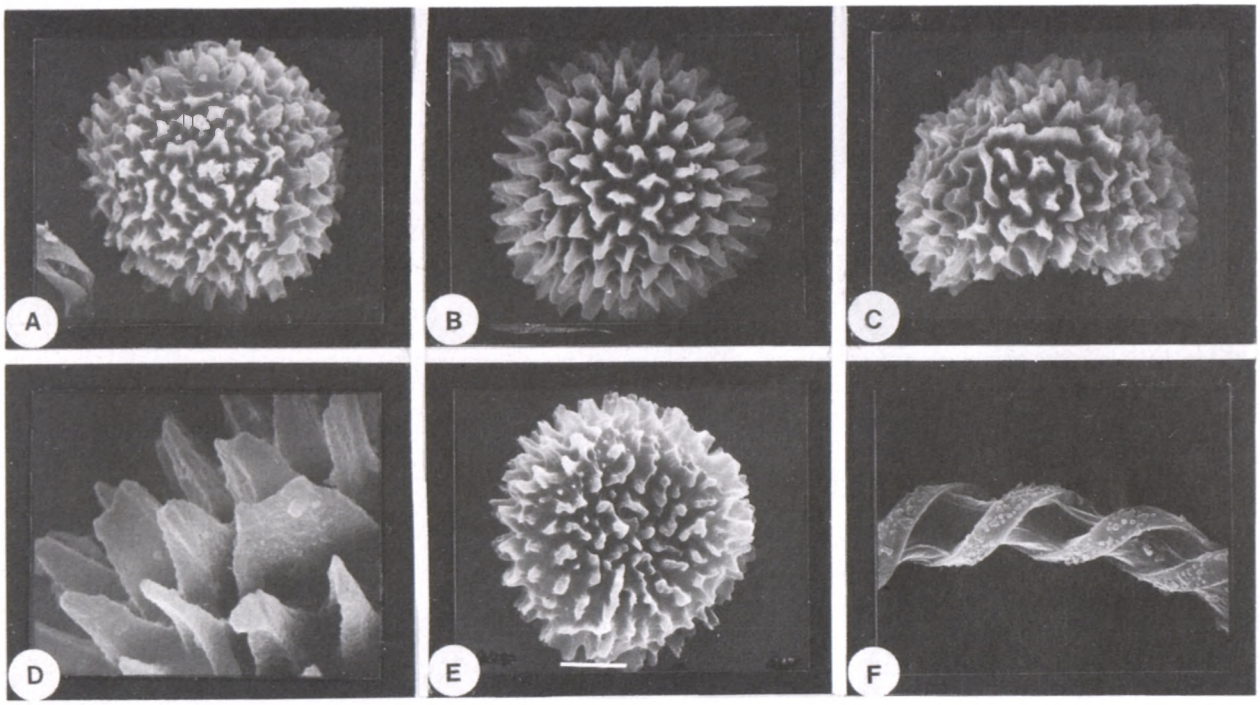

FIGURE 7.—*Fossombronia leucoxantha*. A–E, spores: A, B, distal face; C, side view of distal face; D, detail of spinous processes at margin of distal face; E, proximal face. F, detail of part of elater. A, *Ecklon s.n.* (W) *7693*; B, D, *S.M. Perold 3345*; C, *Ecklon s.n.* (S) L. 29; E, *Oliver 9225*; F, *S.W. Arnell 247*. A, × 742; B, × 642; C, × 835; D, × 2196; E, × 802; F, × 1477.

made no further reference to the former in his book, although there are specimens held at BOL, PRE and S that he had identified as *F. leucoxantha*. Scott & Pike (1987b) have already drawn attention to the confusion between *F. leucoxantha* and *F. tumida*. They also state that 'Arnell's own specimens which he had identified as *F. leucoxantha* 'L. & L'. are mostly *F. spinifolia* St.'. This assumption is incorrect: they had no knowledge of the spore morphology of *F. spinifolia*, as they had overlooked a capsule with ripe spores in the type specimen. *Fossombronia spinifolia* has spores with short irregular lamellae and very few spines. It also is a small plant and has been treated in a previous paper in the current series (Perold 1997c). Scott & Pike (1988) expressed the opinion that the spores 'of what we take to be this species (i.e. *F. spinifolia*) are very similar to those of *F. crispa* '(p. 199) and 'apparently identical,' (p. 193) (see their figs 5 & 6 of spinose spores from the BM sheet, top right corner). The spores which Scott & Pike (1988: figs 27 & 28) illustrate under *F. spinifolia* belong to *F. leucoxantha*. Their spore micrographs of the lectotype of *F. leucoxantha* (Scott & Pike 1987b: figs 3 & 4) depict spines and some ridges and are marginally different from mine (see Figure 7A–E in this paper), but are nevertheless still within the acceptable range of variation in spore ornamentation that I found in the many spore micrographs that I took of this species.

Stephani (1900) recognized three southern African species with spinose spores, *F. spinifolia*, the so-called *F. crispa* and *F. leucoxantha*. He did not have the opportunity to examine spore-bearing material of *F. leucoxantha* and *F. tumida* which he confused with each other; Sim (1926) recognized two species with spinous spores, *F. crispa* with 'long papillae' and *F. leucoxantha* with 'short papillae' in which he followed Stephani; Arnell (1963) placed *F. leucoxantha* (*sensu*) Steph. in synonymy under *F. tumida*, treating *F. crispa* as the only species with spinous spores; Sérgio (1985) accepted *F. crispa* as having spinose spores and *F. zeyheri* as having reticulate spores; Scott & Pike (1988) retained *F. crispa* as a species with spinose spores and thought that Arnell's earlier determinations of *F. leucoxantha* were actually *F. spinifolia*.

3. **Fossombronia tumida** *Mitt.* in Journal of the Linnean Society 16: 193 (1878); Sim: 35 (1926); S.W. Arnell: 80 (1963). Type: Cape of Good Hope, 'on damp ground near the pine plantation at the foot of the Lion's Head, near the beginning of the Kloof road, Cape Town', *Rev. A.E. Eaton* (Aug. & Sept. 1874) (NY, holo.!; W*6447*, iso.!).

Plants in densely crowded or loosely scattered colonies, pale green, becoming white, often tinged with violet-red or with scattered small red flecks; medium-sized to quite robust; shoots simple, 5–12 mm long, 1.1–1.8 mm high, 1.0–2.5(–3.0) mm wide, or once (Figure 9A), rarely twice furcate, terminal segments closely to moderately divergent, ± 3 mm long. *Stems* prostrate, plano-convex in cross section, apically (Figure 8I) 300–440 µm (up to 15 cell rows) high, 530–730 µm wide, tapering proximally and toward base (Figure 8J), 420 µm high, 480 µm wide, pale green to yellowish, sometimes ventrally purple, occasionally with a lateral bud. *Rhizoids* purple, 12.5–20.0 µm wide, some with internal mycorrhizal threads. *Leaves* (Figure 8A–E) overlapping (Figure 9C), suberect, flaccid, very concave, appearing inflated, in terminal segments apices from opposite sides of stem incurved over one another (Figure 9B), obliquely inserted, proximal (trailing) edge almost mid-dorsal on stem, distal (leading) edge lateral, rounded to somewhat irregular, rarely with an appendage at proximal edge, shorter than wide, apically smaller, 675–800 × 1425–1625 µm, covered and preceded by mostly larger, billowing, older leaves, 850–1575 × 1450–2250 µm; mar-

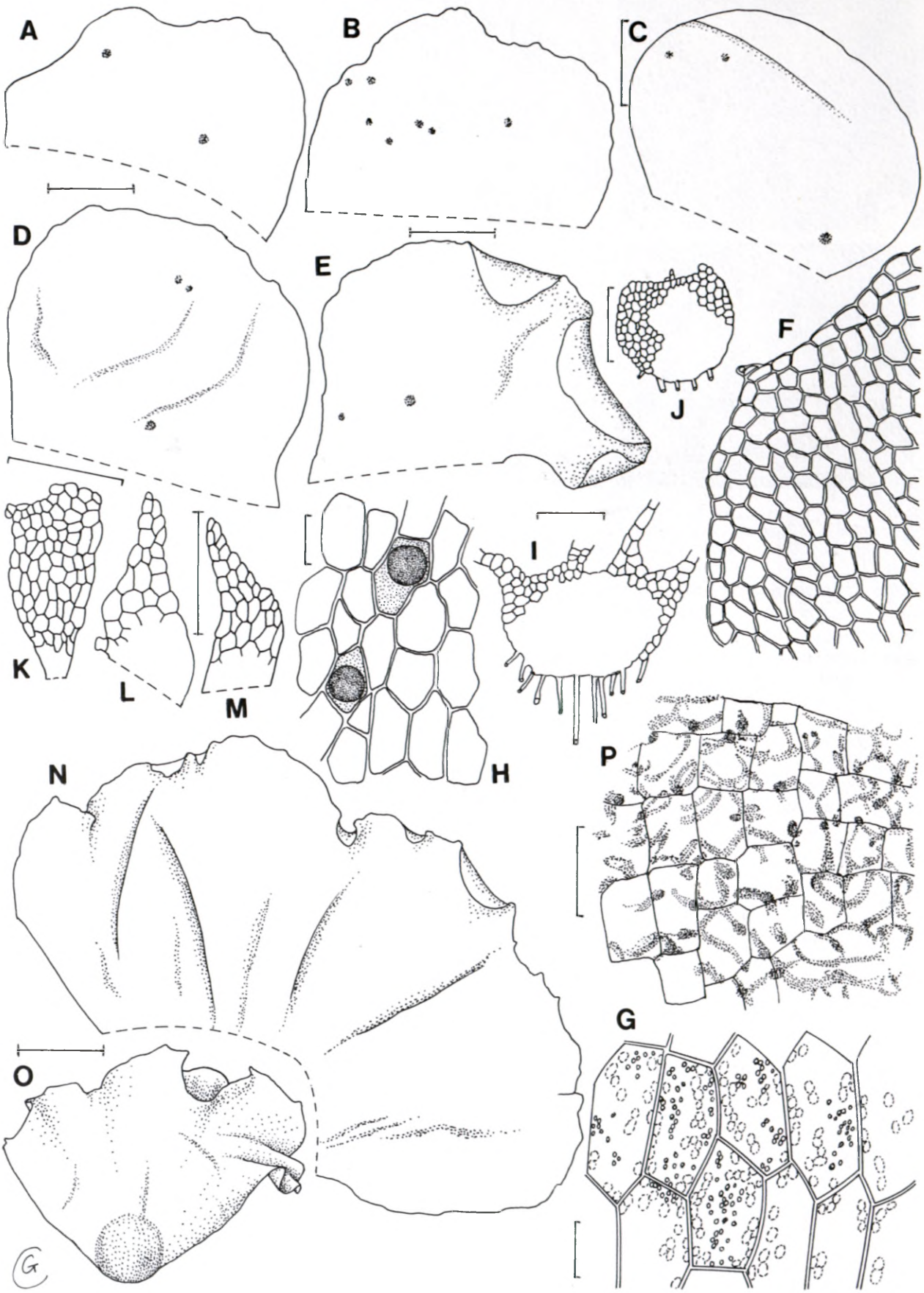

FIGURE 8.—*Fossombronia tumida*. A–E, leaves; F, detail of leaf margin; G, median leaf cells with oil bodies (solid lines) and chloroplasts (dotted lines); H, scattered red-stained leaf cells with dark round body; I, cross section of stem apex; J, cross section of stem base; K–M, bracts; N, opened pseudoperianth; O, pseudoperianth from side; P, cells in capsule wall. A–C, E, G, J, O, *Lübenau-Nestlé SA 425*; D, F, I, *C. M. van Wyk 1494*; H, N, P, *Garside 6109*; K, L, M, *Garside 8335*. Scale bars: A–E, N, O, 500 µm; F–H, P, 50 µm; I–M, 250 µm. Artist: G. Condy.

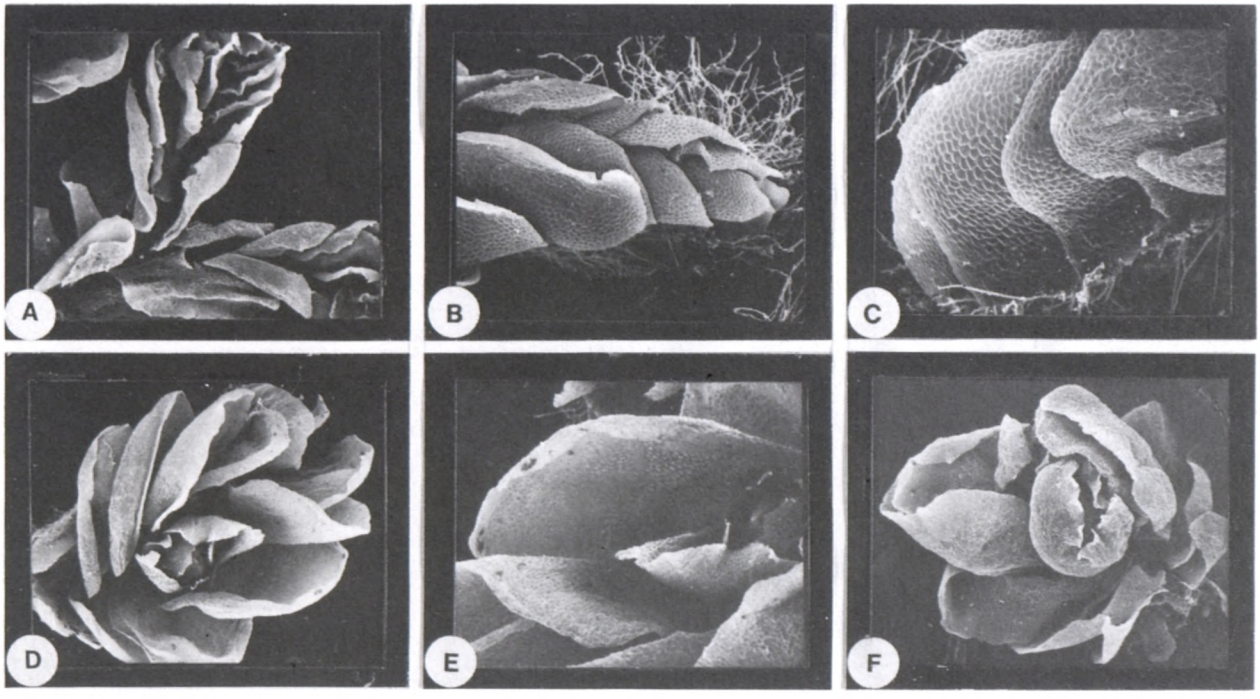

FIGURE 9.—*Fossombronia tumida*. A, branched stem; B, apex of branch with tightly inflexed leaves seen from above; C, overlapping leaves seen from the side; D, leaves and young pseudoperianth seen from above; E, young pseudoperianth seen from side; F, pseudoperianth with mouth inflexed. A, D–F, *Garside 6109*; B, C, *Lübenau-Nestlé SA 425*. A, × 6.6; B, × 15.6; C, × 25; D, × 8; E, × 14; F, × 9.

gins entire, sometimes becoming eroded at upper edge, with up to 9, usually well-spaced slime papillae, ± 17.5 × 17.5 µm, occasionally raised on a basal cell, ± 10.0 × 22.5 µm. *Leaf cells* thin-walled, at upper margins (Figure 8F) subquadrate to rectangular across, 27.5–50.0 × 37.5–55.0 µm, at lower lateral margins long-rectangular, 87.5–112.5 × 12.5–20.0 µm, upper laminal cells 5- or 6-sided, 55.0–75.0 × 45.0–50.0 µm, middle laminal cells 87.5–100.0 × 50.0–62.5 µm, basal cells 80.0–87.5 × 47.5–52.5 µm; scattered throughout some leaves, single cells often stained red and containing a dark, round, internally granular body, rarely 2, up to 50 µm in diameter (Figure 8H). *Oil bodies* rounded, (Figure 8G) oval or irregular in shape, minute; chloroplasts mostly lost in the material examined or clumped together at cell margins.

Dioicous. *Male plants* seemingly scarce, generally longer and narrower than females with pseudoperianths, but gametangia hidden by inflexed leaves. *Antheridia* dorsal on stem, between leaves, globose, short-stalked, ± 150 µm in diameter, each one subtended by a small, ± triangular perigonial bract (Figure 8K–M), 250–400 × 120–170 µm, cells in interior 5- or 6-sided, 37.5–45.0 × 25.0–27.5 µm. *Archegonia* naked, in an interrupted, irregular row along stem. *Pseudoperianths* (Figure 8N, O) on female plants which are simple, inflated, subglobular 'balls' (Figure 9D), ± 5 × 3 mm, with leaves up to 2500 × 3375 µm, mostly single, rarely two in a row, almost sessile, turbinate, rather shorter than or as tall as leaves, 1375 µm long, basally ± 750 µm wide, then quickly flaring above (Figure 9E), ± 2250 µm wide across mouth, occasionally inflexed (Figure 9F), irregularly and shallowly lobed, sometimes with projecting longitudinal 'seam' on inside; cells not appreciably different in shape and size from those of leaves. *Capsules* globose, ± 1000 µm in diameter, wall bistratose, cells of inner layer (Figure 8P) irregularly shaped, 22.5–60.0 × 22.5–25.0 µm, each cell wall with ± 3 yellow-brown, nodular and semi-annular thickenings or sometimes entire wall thickened. *Seta* ± 400 µm long, 250 µm in diameter. *Spores* brown, 45–55 µm in diameter, including marginal lamellae; hemispherical; distal face (Figure 10A, B) convex, with rather wavy, ± parallel lamellae, (Figure 10C), 5.0–7.5 µm high, projecting at periphery (Figure 10D), over polar area anastomosing to form few to many (± 36) areolae, 2.5–5.0 µm wide; proximal face (Figure 10E) lacking triradiate mark, flat, covered with irregularly curving and branching ridges, (sometimes markedly raised), and a few coarse papillae, ± 28 'spines' projecting around spore periphery, not connected by perispore. *Elaters* (Figure 10F) yellow-brown, 152.5–200.0 µm long, 10 µm wide in centre, tapering to looped tips, 5 µm wide, smooth, bispiral or partly trispiral.

Fossombronia tumida grows on damp, rather sandy soil at Lion's Head, the Round House, Kloofnek, Stellenbosch Flats and at Roman River, south of Wolseley (Figure 4). A specimen, *Wager 39* (CH 3703) is said to be from East London, but this locality could be wrong. Sim (1926) observed that it is found in S.W. (meaning Western Cape) localities, 'but not seen eastward'. This species is by no means common.

Fossombronia tumida is distinguished by its inflated or tumid appearance and very concave leaves, with small, scattered red flecks containing round bodies. The spores are generally reticulate over the distal pole, and the outer areolar walls break down into lamellae which continue to the margin.

Scott & Pike (1987b) regard *F. tumida* as very similar vegetatively to *F. intestinalis* Tayl. from Australia and Tasmania, but 'with experience, however, they can be separated. The former is larger, with flaccid leaves often tinged with purple-brown and with entire instead of slightly denticulate leaves. The spores are quite distinct'.

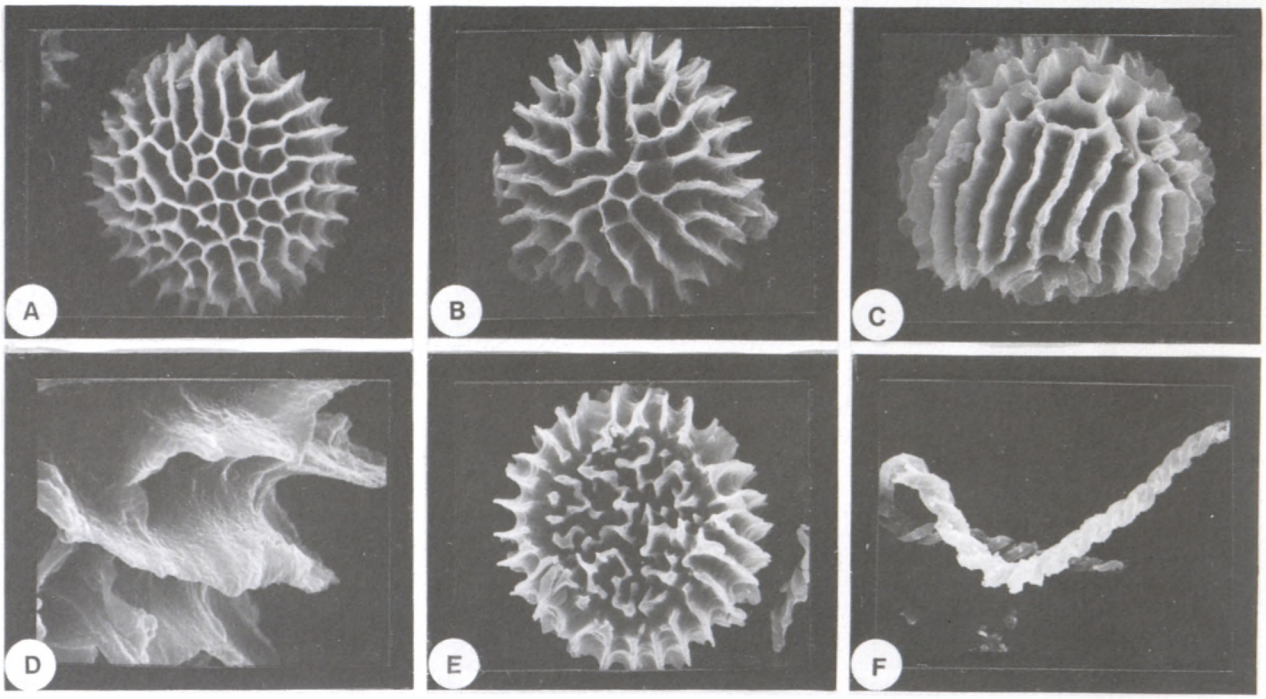

FIGURE 10.—*Fossombronia tumida*. A–E, spores: A, B, distal face; C, side view of distal face; D, detail of lamellae at margin of distal face; E, proximal face. F, elater. A, E, *Garside 6109*; B, D, *Garside 8335*; C, F, *Duthie CH1580*. A, × 659; B, × 562; C, × 642; D, × 2356; E, × 672; F, × 356.

Scott (1985) claims that *F. intestinalis* also occurs in southern Africa, but does not cite a particular specimen. I have not found it so far. The confusion between *F. tumida* and *F. leucoxantha* is discussed above under the latter species.

SPECIMENS EXAMINED

With one exception, only fertile specimens are included; held at PRE, unless otherwise indicated.

S.W. *Arnell 39*, *46*, *116* (2) BOL, *149* (2) BOL, *199* (2) BOL, *247* (2), *266* (2) BOL; *274* (2), *275* (2) BOL, *282* (2), *384* (2) BOL, *626* (2) BOL, *941* (2) BOL, *1118* (2) BOL, *1205* (2) S, *2161*, *2181* (1) BOL, *2184*, *2201* (1).

Bottomley CH 3567 (1). *Breutel* herb. no. *024665* (2) G.

Duthie CH 1580 (3).

Eaton (3) NY (holo.), herb. no. *6447* (3) W (iso.). *Ecklon* ex herb. Dr Winter, herb. no. *024660* (1) G; L. 29 (lecto.) (2) S; (isolecto.) (2) E; herb. no. *7693* (2) W; *64* (?syntype) (2) BM; herb. no. *7692* (3) W.

Garside 6109 (3) BOL; *6218* (2) BOL, *6463* (2) BOL, *6488* (2) BOL, *6498a* (2) BOL; *6498* (3) BOL; *6703* (2) BOL, *6707* (2) BOL; *6722* (2) BOL; *8335* (3) PRE. *Garside & Arnell 115* (2). *Glen 2258*, *2261a* (1).

Lübenau-Nestlé SA3 (2), *14* (1), *SA425* (3) private herb.

Oliver, E.G.H. 9225 (2).

S.M. Perold 65, *2704*, *2457*, *2887* (sterile, det. E.W. Jones as *F. zeyheri*), *3280* pp., *3317* (1); *3329*; *3331*, *3332*, *3337*, *3340*, *3341*, *3344*, *3345*, *3355* (2); *3444* (1). *S.M Perold & Koekemoer 3282*, *3606*, *3615* (1). *S.M. Perold & Van Rooy 3558*, *3567* (1). *Pillans 4241* (1) BOL.

Reichenbach herb. no. *354138* (1) W. *Reinecke CH182* (1). *Rehmann* herb. no. *5578* (3) W.

Schelpe 5160 (1) BOL. *Sim CH1587*, *CH1616*, *CH1633*, *CH1634*, *CH1645*, *CH1648* (1). *Sprengel* L. 32, no. *244* (1) S. *S. Strauss*, *134a*, *209*, *CH13664* (1).

C.M. Van Wyk, *1494* (3). *J. Victor*, *1379*, *1380* (1).

H.A. Wager, *27*, *28* (1); *39* (3). *V.A. Wager*, *112* (1). *Wilms 2538* (3) W.

Zeyher herbarium sheet, top row: left corner, middle, lower row: left BM, ex herb. Moricand no. *481* herb. no. *024661* (G), Flora Cap. no. *482* S, herb. no. *024663* G, ex herb. Rabenhorst herb. no. *024669* G, ex herb. (?)ope herb. no. *024670* G, Flora Cap. no. *482* G herb. no. *024676* G (1).

Without collector's name

Cap (3 written on packet in pencil) STR, lecto., ex herb. Lehmann S, ex herb. Karl Müller S, Gottsche dedit. herb. no. *024659* G, ex herb. de Candolle ex herb. Müll. herb. no. *024662* G, Jack dedit. herb. no. *024664* (1) G.

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REFERENCES

ARNELL, S.W. 1963. *Hepaticae of South Africa*. Swedish Natural Science Council, Stockholm.

GOTTSCHE, C.M., LINDENBERG, J.B.G. & NEES AB ESENBECK, C.G. 1844–1847. *Synopsis hepaticarum*. Meissner, Hamburg.

LEHMANN, J.G.C. 1829. Hepaticarum capensium a C.F. Ecklon. *Linnaea* 4: 357–371.

MITTEN, W. 1878. List of Hepaticae collected by Rev. A. E. Eaton at the Cape of Good Hope (Aug. & Sept. 1874). *Journal of the Linnean Society (Botany)* 16: 187–197.

PEROLD, S.M. 1997a. Studies in the liverwort genus *Fossombronia* (Metzgeriales) from southern Africa. 1. Three new species from Gauteng, Northern Province and Mpumalanga. *Bothalia* 27: 17–27.

PEROLD, S.M. 1997b. Studies in the liverwort genus *Fossombronia* (Metzgeriales) from southern Africa. 2. An amendment to three species from Western Cape, described by S.W. Arnell. *Bothalia* 27: 29–38.

PEROLD, S.M. 1997c. Studies in the liverwort genus *Fossombronia* (Metzgeriales) from southern Africa. 3. An amendment to *F spinifolia*. *Bothalia* 27: 39–42.

PEROLD, S.M. 1997d. The lectotypification of *Fossombronia crispa*. *Bothalia* 27: 137–139.

SCOTT, G.A.M., 1985. *Southern Australian liverworts*. Bureau of Flora and Fauna, Canberra.

SCOTT, G.A.M. & PIKE, D.C. 1987a. The *Fossombronia foveolata* complex. *Lindbergia* 13: 79–84.

SCOTT, G.A.M. & PIKE, D.C. 1987b. Studies on *Fossombronia* in Australia 3. Taxonomic and nomenclatural problems. *Journal of the Hattori Botanical Laboratory* 63: 99–105.

SCOTT, G.A.M. & PIKE, D.C. 1988. Revisionary notes on *Fossombronia*. *The Bryologist* 91: 193–201.

SÉRGIO, C. 1985. Notulae Bryoflorae Lusitanicae 1. 5. Notas Acerca do género *Fossombronia* Raddi em Portugal. *Portugaliae acta biologica* (B) 14: 181–198.

SIM, T.R. 1926. The Bryophyta of South Africa. *Transactions of the Royal Society of South Africa* 15: 1–475. Cape Town.

STEPHANI, F. 1900. *Species hepaticarum* Vol. 1. Geneva.

STEPHANI, F. 1985. *Icones hepaticarum*, microfiche. Inter Documentation Company bv, Leiden.