

Studies in the Marchantiales (Hepaticae) from southern Africa. 9. The genus *Marchantia* and its five local species

S.M. PEROLD*

Keywords: distribution, ecology, Hepaticae, *Marchantia*, *M. berteriana*, *M. debilis*, *M. paleacea* subsp. *paleacea*, *M. pappeana* subsp. *pappeana*, *M. polymorpha* subsp. *ruderalis*, southern Africa, taxonomy

ABSTRACT

In this, the ninth and final article in the series on southern African Marchantiales, a taxonomic account is given of the genus *Marchantia* which is locally represented by five species. Two of the three subgenera that are recognized, namely subgenus *Marchantia* (with two species, *M. polymorpha* subsp. *ruderalis* and *M. berteriana*), as well as subgenus *Chlamidium* (Corda) Bischl. which is divided into three sections, namely *Paleaceae* (with *M. paleacea* subsp. *paleacea*), *Chlamidium* (with *M. pappeana* subsp. *pappeana*) and *Papillatae* (with *M. debilis*) are treated. The third subgenus, *Protomarchantia* Schust., is absent from the region. Corrections need to be made to the *Marchantia* species given in Magill & Schelpe's (1979) checklist and in Arnold & De Wet (1993). Descriptions and illustrations of the taxa together with distribution maps, their ecology and a key to the subgenera and species are provided.

Only traditional taxonomic methods were employed and this treatment closely follows that of Bischler-Causse (1993a), the recognized world authority on the group. All southern African specimens held at BOL and PRE, as well as a few from other herbaria have been studied and some new collections have been added. It is shown that *M. polymorpha* subsp. *ruderalis* has been introduced, as it is only known from local nurseries. The presence here of *M. paleacea* subsp. *paleacea* is confirmed, although it is rare. Otherwise little that is new could be added to the exhaustive studies by Bischler-Causse (1993a).

UITTREKSEL

In hierdie, die negende en finale artikel in die reeks oor die Marchantiales van suidelike Afrika, word 'n taksonomiese verslag gegee oor die genus *Marchantia* wat plaaslik deur vyf spesies verteenwoordig word. Twee van die drie erkende subgenusse, nl. subgenus *Marchantia* (met twee spesies, *M. polymorpha* subsp. *ruderalis* en *M. berteriana*) sowel as subgenus *Chlamidium* (Corda) Bischl. wat verdeel word in drie seksies, nl. *Paleaceae* (met *M. paleacea* subsp. *paleacea*), *Chlamidium* (met *M. pappeana* subsp. *pappeana*) en *Papillatae* (met *M. debilis*), word behandel. Die derde subgenus, *Protomarchantia* Schust., kom nie in die gebied voor nie. Regstellings moet aangebring word aan die *Marchantia*-spesies soos aangegee in Magill & Schelpe (1979) se lys en in Arnold & De Wet (1993). Beskrywings en illustrasies van die taksons sowel as verspreidingskaarte, die ekologie en 'n sleutel tot die subgenusse en spesies word verskaf.

Slegs tradisionele taksonomiese metodes is toegepas, en word die werk van Bischler-Causse (1993a), die erkende wêreld-gesaghebbende op die groep, word ten nouste nagevolg in hierdie behandeling. Alle eksimplare uit suidelike Afrika in BOL en PRE asook 'n paar van ander herbariums is bestudeer en nuwe versamelings is bygevoeg. Daar word aangetoon dat *M. polymorpha* subsp. *ruderalis* uitheems is, aangesien dit slegs in plaaslike kwekerye voorkom. *M. paleacea* subsp. *paleacea* se teenwoordigheid hier word bevestig, maar dit is skaars. Orens kon min tot die uiters volledige studies deur Bischler-Causse (1993a) bygevoeg word.

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Marchantia L., Species plantarum edn 1: 1137 (1753) emend. Raddi, Opuscoli Scientifica di Bologna: 358 (1818); Sim: 27 (1926); S.W. Arnell: 53 (1963); Bischl.: 6 (1984); Bischl.: 13 (1989a); Bischl.: 13 (1993a); R.M. Schust.: 305 (1992). Type species: *Marchantia polymorpha* L. [lecto. fide Leman: 115 (1823)].

Marchantia M. Marchant f.: 229 (1739).

Marchantiopsis Douin & R.C.V. Douin: 135 (1918).

Chlamidium Corda: 647 (1829).

Thalloid, smallish to medium-sized to large, flat and ungrooved, relatively delicate or firm and occasionally rather leathery, green to dark green or greyish green, along margins sometimes purplish, rarely all over dorsally and occasionally also ventrally; dorsal face with distinct polygonal areolae, each with a pore; in crowded mats, sometimes in partial rosettes, hygrophytes, requiring high humidity and mostly unable to sustain life dry; growing

* National Botanical Institute, Private Bag X101, Pretoria 0001
MS. received: 1995-03-27.

on damp soil of vertical stream banks, at waterfalls, dams, weirs and canals, sometimes on wet rocks, rarely on rotting wood.

Branches broadly band- or narrowly ribbon-shaped, pseudodichotomously furcate, without lateral or apical innovations from keel, ventrally thickened medianly and tapered toward margins, which are lobulate, crenulate, undulate or entire, apex notched, with median scale appendages recurved over edge. *Dorsal epidermal cells* generally unistratose, often without chloroplasts, walls thin or slightly thickened but lacking trigones; air pores compound, encircled by several superimposed concentric rings of cells, some above epidermis, others projecting into air chambers below, the latter in a shallow, single layer, densely packed with 2–4(5)-celled assimilatory filaments; storage tissue compact, sometimes with a few sclerotic cells and/or mucilage cavities, also with scattered oil cells each containing a single, large oil body, these present as well elsewhere in thallus and scales; numerous rhizoids ventrally, some smooth, others pegged, rarely with inner thickenings spirally connected. *Ventral scales* in 4 or more rows, covering part or all of ventral face and rarely projecting beyond margins, median scales bluntly triangular, constricted where joined to appendage, laminal scales smaller, sometimes in double rows, lacking an appendage, marginal scales rarely present. *Cupules* borne dorsally on thalli, hollowed, contracted below, flaring above, margin ciliate, lobed-ciliate, dentate or nearly entire, containing discoid gemmae that reproduce vegetatively.

Dioicous. *Gametangiophores* stalked. *Stalks* arising at apex of main and/or lateral branches, basally sometimes surrounded by large scales, generally without an appendage, along their length bearing filiform scales, 2–4 rhizoid furrows and 0–2 bands of air chambers with compound air pores. *Antheridiophores* with receptacular discs rather flat, lobed or divided into rays, antheridia and compound air pores on dorsal side, several rows of scales per lobe beneath. *Archegoniophores* with receptacles convex above, lobed or divided into \pm flat rays, dorsally with compound air pores, below with scales and archegonia, each one surrounded by calyptra and pseudoperianth, in groups that are enclosed by bivalved involucre, occurring alternate with the lobes or rays (in African species). *Sporophytes* consisting of foot, short seta (elongating later) and subglobose capsule, its unistratose wall with annular thickenings, dehiscing irregularly. *Spores* small, thin-walled, \pm triangular-globular, ornamentation with numerous thin, irregularly convoluted ridges or with few wide ridges separated by granules, the 2 faces similar or dissimilar. *Elaters* tapering at ends, bi- or trispiral. *Chromosome number*: $n = 9$ (basically).

On the basis of differences in spore morphology, germination patterns and flavonoid patterns, the genus is subdivided into 3 subgenera: *Marchantia*, *Chlamidium* and *Protomarchantia* R.M. Schust. The latter is absent from the region.

Key to local subgenera, sections and species

- 1a Thalli with margins plicate-crested, crenulate or lobulate, dorsally with or without dark median band; epidermal pores with walls of cells bordering inner opening slightly or strongly projecting and pores then cruciate; scales in 4–6 rows, covering $\frac{3}{4}$ or all of ventral surface and then also extending beyond thallus margins; appendages of median scales orbicular or reniform or ovate, marginal cells slightly or strikingly smaller than inner cells; laminal scales much wider than long; cupules with ciliate lobes at margins, externally with papillae; male receptacles peltate, shallowly dissected into 6–10 broad lobes; membranous margins of rays crenulate or entire and then with very small cells; female receptacles deeply dissected into 9–11 terete rays, with or without papillae; stalks with single broad band of air chambers; margins of involucre with ciliate lobes; spores 8–16 μm in diameter, ornamentation on 2 faces similar, with numerous narrow convoluted ridges subgenus **Marchantia** (p. 185):
- 2a Thalli with margins entire or crenulate, crested-plicate; dorsally often with dark median band; cells bordering inner opening of epidermal pores with slightly convex inner walls, pores not cruciate; ventral scales in 6 rows and extending beyond thallus margins; appendage of median scales small, margins bordered with somewhat smaller cells; membranous margin of male receptacle crenulate, composed of slightly smaller cells; rays of female receptacle with numerous papillae 1. *M. polymorpha*
- 2b Thalli with margins lobulate; dorsally without dark median band; cells bordering inner opening of epidermal pores with strongly convex inner walls and pores cruciate; ventral scales in 4(–6) rows and not extending beyond thallus margins, marginal scales sometimes partly or altogether absent; appendage of median scales large, margins entire or slightly crenulate, bordered with strikingly small marginal cells; membranous margin of male receptacle not distinctly crenulate, composed of very small cells; rays of female receptacle without papillae 2. *M. berteriana*
- 1b Thalli with margins entire, nearly flat or sometimes slightly undulate, dorsally with or without dark median band; cells bordering inner opening of epidermal pores with straight or convex walls, rarely with strongly projecting processes and then pores cruciate; scales in 4 rows, covering $\frac{1}{4}$ to almost $\frac{2}{3}$ of ventral surface; appendage of median scales orbicular, ovate or \pm triangular, apically acuminate, acute or apiculate, marginal cells smaller than inner ones; laminal scales as long as or longer than wide; cupules with margins ciliate, almost entire or rarely with ciliate lobes, externally rarely with papillae; male receptacles palmate or rarely peltate, shallowly or deeply dissected into rays; membranous margin of lobes entire or slightly crenulate; female receptacles dissected into 5–9 apically \pm flat lobes; margins of involucre ciliate or entire, rarely with ciliate lobes; stalks with air chambers in 1 or 2 bands; spores 20–35 μm in diameter, ornamentation on 2 faces dissimilar, distally mostly with wide ridges subgenus **Chlamidium** (p. 192):
- 3a Thalli medium-sized to large, 6–8(11) mm wide; epidermal pores with inner walls of cells bordering inner opening strongly projecting and pores cruciate; appendages of median scales with margins entire or slightly denticulate; cupules with triangular, ciliate lobes and externally with numerous papillae; female receptacle deeply dissected into lobes, apically truncate or emarginate; margins of involucre with ciliate lobes section **Paleaceae** (p. 192), 3. *M. paleacea*
- 3b Thalli smallish to large, 3.5–10.0 mm wide; epidermal pores with inner walls of cells bordering inner opening straight or convex; appendages of median scales with margins often distinctly toothed; cupules bearing long or short cilia or almost entire at margins and externally without or with few papillae; female receptacle shallowly or deeply dissected into lobes; margins of involucre ciliate or \pm entire:

- 4a Thalli 6.0–8.5 (–10.0) mm wide; dorsally without dark median band; appendages of median scales large, 520–550 × 375–530 µm, inner cells also comparatively large, 75.0–87.5 × 32.5–42.5 µm, i.e. cell structure loose; margins of cupules with cilia up to 6 cells long; female receptacle large, shallowly dissected into broad lobes, sometimes bearing a male ray; margins of involucre ciliate section *Chlamidium* (p. 195), 4. *M. pappeana*
- 4b Thalli 3.0–7.5 mm wide; mostly with distinct dark median band dorsally; appendages of median scales small, 350–375 × 275–340 µm, inner cells not markedly 'loose', cells 67.5–75.0 × 30.0–37.5 µm; margins of cupules crenulate or with short cilia, up to 3 cells long; female receptacle rather small, deeply dissected into narrow lobes; margins of involucre entire or crenulate section *Papillatae* (p. 199), 5. *M. debilis*

Subgenus *Marchantia*

Marchantia L. sect. *Astromarchantia* Nees; 60, 61 (1838) (nom. illegit.)

Marchantia L. (without rank) *Stellatae* Gottsche, Lindb. & Nees; 522 (1844–1847; published 1846)

Marchantia L. (without rank) *Marchantiotypus* Dumort.; 150 (1874).

Thallus branches wide, from nearly 7 mm to almost twice as wide; margins crenulate, lobulate or plicate-crested. *Dorsal epidermis* with or without papillae; air pores surrounded by 4–5(6) concentric rings of cells, at inner openings sometimes with rounded walls, otherwise with pronounced processes and pores then cruciate; storage tissue lacking sclerotic cells. *Scales* in 4–8 rows, covering $\frac{3}{4}$ to all of ventral face, containing scattered oil cells; median scales with appendages, ovate, orbicular or reniform, not acuminate at apex; margins crenulate, toothed or entire, sometimes with a row of cells very much smaller than those in interior; laminal scales wider than long, on either side of median scales, apically rounded, lacking papillae, upper cell walls with trigones. *Cupules* with acutely triangular, toothed lobes, externally papillate.

Dioicous. *Antheridiophores* with receptacles ± symmetrical, peltate, rays very short and broad; stalks with 2 rhizoid furrows, but lacking air chambers. *Archegoniophores* with receptacle deeply dissected into terete lobes; stalks with 2 rhizoid furrows and a single band of air chambers; involucre with toothed or ciliate margins. *Spores* small, 8–16 µm in diameter; 2 faces similarly ornamented, with numerous thin, highly convoluted ridges, triradiate mark distinct to absent and wing absent.

Marchantia polymorpha, *M. berteriana* and *M. plicata* (from central and South America) are classified in subgenus *Marchantia*.

1. *Marchantia polymorpha* L. in *Species plantarum* edn 1: 1137 (1753); Bischl.: 34 (1993a). Type: Europe, *Dillenius* in *Historia Muscorum*, t. 76, fig. 6E, F (1742) [OXF, lecto., typo., fide Bischl. & Boisselier-Dubayle; 363 (1991) (photo. of typo. in PRE!)].

Synonymy after Bischler-Causse (1993a).

Thallus large, mostly prostrate, sometimes growing somewhat erect, apical segments broadly obovate, bright or dark or yellowish green, medianly with or without dark, continuous or interrupted band dorsally (Figure 1A), margins reddish brown, crisped, entire, sometimes crenulate; pores quite small to large, subdorsal air chamber walls visible from above; margins not raised and incurved when

dry; in crowded, overlying patches, repeatedly pseudodichotomously furcate. *Branches* with total length up to 35 mm, terminally 2–15 mm long and successive branches 5–10(–14) mm apart, narrowly divergent to overlapping, 7–10 mm wide, 325–375 µm thick over midrib, laterally thinning out into wings, apex notched, with appendages of several purple-red median scales recurved over edge; margins acute, thin, becoming recurved, flanks sloping obliquely, ventral face medianly keeled (Figure 1C), densely covered with rhizoids and on either side with 3 rows of purple or brownish scales, the outermost extending beyond thallus margins (Figure 1B).

Dorsal epidermal cells unistratose, mostly hyaline, 4–6-sided, 35–74 × 18–30 µm, thin-walled, lacking trigones, in transverse section 18–20 µm thick, marginal cells in 3(4) rows (Figure 1G), those in outer 1 or 2 rows smaller, generally rectangular, 15.0–27.5 × 17.5–20.0 µm, inner cells larger, 27.5–37.5 × 22.5–27.5 µm; air pores quite numerous, 175–350 µm distant from each other, raised, compound, round or oval, 30.0–62.5 × 40.0–60.0 µm, surrounded by 4 or 5 concentric rings of cells, 2 or 3 above epidermis and 2 or 3 projecting into air chambers (Figure 1F), innermost ring of upper cells collapsed, ± 5 µm wide, next ring of cells ± 40 × 10 µm, outer ring of cells ± 50 × 12 µm, partly overlying epidermal cells (Figure 1D), inner opening mostly surrounded by 4 cells (Figure 1E), ± 27.5 µm long, and ± 12.5 µm wide across widest parts which protrude into cavity and are covered with black granular deposit. *Assimilation tissue* 50–100 µm thick, $\frac{1}{6}$ – $\frac{1}{3}$ as thick as thallus, air chambers in a single layer, 150–250 µm wide, height of bounding walls 2 or 3(4) cells, round or oval, 17.5–27.5 × 15.0–17.5 µm, chambers internally crowded with densely chlorophyllose, mostly 2- or 3-celled filaments (Figure 1F), cells round, oval, elongated or irregular, 20.0–32.5 × 15.0 µm; storage tissue occupying ± 11 rows of cells in ventral $\frac{2}{3}$ – $\frac{5}{6}$ of thickness of thallus medianly, decreasing laterally, cells angular, 45.0–75.0 × 60.0–65.0 µm, smaller just below air cavities and where adjoining ventral epidermis; sclerotic cells and mucilage cavities absent; rhizoids some smooth, 15–50 µm wide, faintly brown, others tuberculate, 7.5–12.5 µm wide, and still others with internal 'spirals', ± 12.5 µm wide.

Median scales (Figure 1K) pale mauve, in one row on either side of midrib, ± obliquely triangular, body up to 750 µm long, width 1575–2250 µm across nearly straight base, continuing into narrow 'tail', cells in body of scale elongated, 4–6-sided, 85–160 × (25–)40–62 µm, rhizoids arising from a few smaller rhizoid initial cells and with 5 or 6 scattered oil cells present, ± 25.0 × 22.5 µm, toward margins cells changing orientation and some in semiradial groups, from centre of which 1 or 2 papillae project, 35–50 × 10 µm; scale narrowing upwards, deeply constricted where joined with appendage, which is broadly

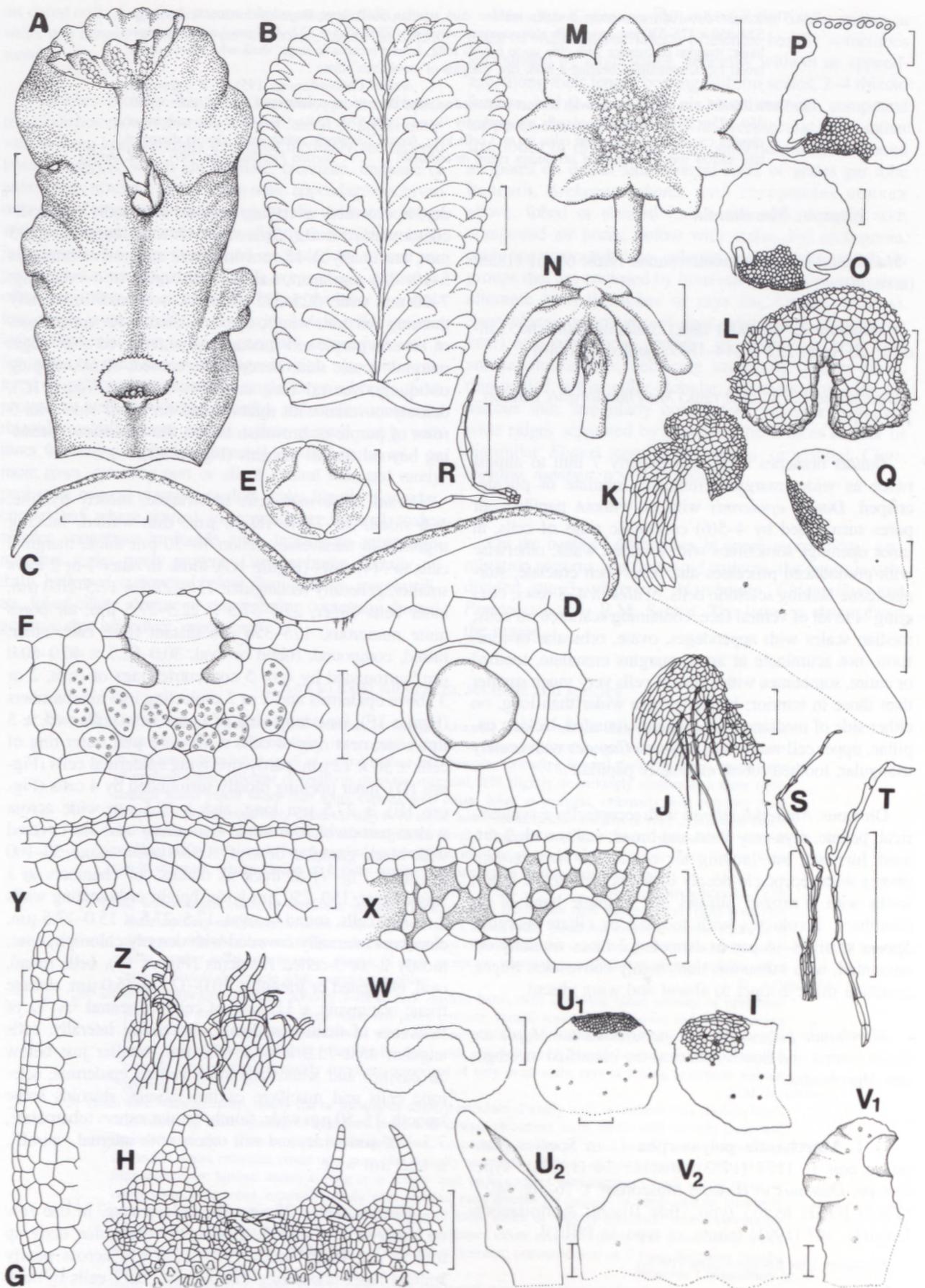


FIGURE 1.—*Marchantia polymorpha* L. subsp. *ruderalis*. A–G, thallus: A, dorsal face of apical branch of ♂ with disc and cupule; B, ventral face of apical branch; C, t.s. of branch; D, air pore and surrounding cells from above; E, air pore from below; F, t.s. of air pore, dorsal epidermal cells and air chamber; G, margin. H, cupule margin; I, marginal scale; J, laminal scale; K, median scale; L, appendage of median scale; M, ♂ receptacle; N, ♀ receptacle from side; O, t.s. of ♂ stalk; P, t.s. of ♀ stalk; Q, median scale of ♂ receptacle. R–V, scale: R, along ♂ stalk; S, ♀ receptacle; T, along ♀ stalk; U₁, U₂, foot of ♂ stalk; V₁, V₂, foot of ♀ stalk. W, t.s. of ♀ ray; X, detail of part of section of ♀ ray, showing papillae on epidermal cells and air chambers; Y, margin of ♂ ray; Z, margin of involucre. A, M, O, Q, R, U₁, U₂, Y, *Perold & Koekemoer* 3248; B–L, N, P, S, T, V₁, V₂, W₁, X, Z, *Glen* 3728. Scale bars: A, B, M, N, 2 mm; C, 1 mm; D–F, 50 μm; G, X, Y, 100 μm; H–L, O–W, 250 μm.

rounded, brown or tinged with purple, (350–) 400–640 × 500–700 µm, central cells 4–6-sided, 42.5–62.5 × 32.5–50.0 µm, with 1–3 oil cells, up to 30.0 × 22.5 µm, margin sharply toothed, crenulate or almost entire, cells small, some conical, ± 22.5 × 15.0 µm, projecting slightly, others rectangular, with long axis parallel to margins, ± 35.0 × 7.5 µm, or perpendicular, with 10 µm high protuberance, sometimes separated as distinct cell, submarginal cells larger, 25.0–27.5 × 20.0–37.5 µm. *Laminal scales* hyaline or pale mauve, in one row on either side of and lateral to median scales, almost wedge-shaped, but with apex rounded, base flatly arched (Figure 1J), 600–825 × 1450–1750 µm, upper cells rather irregularly arranged, some with slightly thickened walls, 4–6-sided, 37.5–42.5 × 17.5–27.5 µm, larger lower down, 70–90 × 30–35 µm, oil cells rare, 5 or 6 rhizoids originating from smaller internal initial cells, at upper margin, several papillae, ± 47.5 × 12.5 µm. *Marginal scales* (Figure 1I) usually projecting beyond thallus margins, hyaline or brownish, oblong or ovate, apex rounded, 700–750 × 550–650 µm, upper cells with walls thickened and brown, ± 47.5 × 32.5 µm, lower down walls not thickened, cells 70.0–120.0 × 25.0–37.5 µm, up to 5 or 6 scattered oil cells and some rhizoid initials present. *Cupules* with ciliate, ± triangular lobes (Figure 1H), ± 240 µm long and 250–275 µm wide at base, apically with 5 or 6 cells in a uniseriate, vertical row, top cell conical, ± 20 × 10 µm, lower cells gradually enlarging, bottom cell trapezoid, ± 27.5 × 32.5 µm, at base of lobes on either side 3 or 4 transversely projecting cellular filaments or cilia, 1–6 cells long, cells ± 35 × 10 µm, lower down cupule wall several cell layers thick, exteriorly with numerous 1–3-celled papillae and internally with many oil cells.

Dioicous. *Antheridiophore* arising from apex of terminal segment (Figure 1A) of main or short lateral branch, raised on stalk, ± 4.5–15.0 mm long, in transverse section rounded, at widest part along its length, ± 975 × 1000 µm (Figure 1O), cortical cells small, 10.0–17.5 × 7.5–20.0 µm, outer wall slightly thickened and bulging, medullary cells larger, angular, 22.5–45.0 × 22.5–35.0 µm, air chambers absent, but with 2 rhizoid furrows, 237.5–250.0 × 87.5–137.5 µm, lined with purple pigmented cells; *scales* at base of stalk (Figure 1U₁, U₂), large, with purple bases, round or oblong, lacking an appendage, 1250–2000 × 800 µm, cells in body of scale, 50.0–57.5 × 20.0–30.0 µm, smaller at apex and margin, 22.5–37.5 × 12.5 µm, sometimes with protruding papillae, up to 8 scattered oil cells present; *scales along length of stalk*, hyaline, filiform (Figure 1R) (1)2–3 cells wide; *receptacle* ± 8 mm in diameter, shallowly dissected into 8(–10) lobes, ± 375 µm long, symmetric (Figure 1M), basal sinus up to 30° wide; margins of lobes (Figure 1Y) membranous, hyaline, crenulate, cells in outer 1 or 2 rows small, 10.0–17.5 × 15.0–22.5 µm, some with a bulging protrusion, inner cells larger, 30.0–72.5 × 32.5–37.5 µm; *median scales* on ventral side of lobes (Figure 1Q) hyaline, oblong with rounded apex and lacking appendage, 1375–1575 × 600–850 µm, cells in body of scale 4–6-sided, 50.0–75.0 × 27.5–30.0 µm, 4–10 oil cells present, ± 25 × 25 µm, upper marginal cells thin-walled, small, 7.5–15.0 × 12.5–15.0 µm, sometimes toward base of lateral margins, with small papillae.

Archegoniophore arising from apex of terminal segment of main or short lateral branch, raised on stalk, 17–40 mm long, in transverse section 1000 × 1250 µm, narrower across

single band of air chambers, ± 625 µm (Figure 1P), cortical cells small, 10.0–20.0 × 7.5–17.5 µm, outer wall slightly thickened, medullary cells angular, 37.5–42.5 × 25.0–32.5 µm, with 2 rhizoid furrows, ± 350 × 250 µm; *scales at base of stalk*, (Figure 1V₁, V₂), large, purple or brown or hyaline, rarely with slightly constricted appendage, mostly without, but some appear to be composite scales, shape irregular, up to 750 × 1000(–1750) µm, inner cells ± 50 × 45 µm, small at crenulate upper margin, 17.5–25.0 × 12.5–27.5 µm, at lateral margins toward base, sometimes with papillae, ± 35 × 15 µm; *scales along length of stalk* (Figure 1T), hyaline or brown, filiform, up to 600 µm long, apical cell conical, ± 55.0 × 12.5 µm, lower 2(3) cells ± 62.5 × 20.0 µm, serially arranged and then 2 adjacent, sometimes with base of upper cell wedged between them, and sometimes with a short lateral branch; *receptacle* 9.5–10.0 mm in diameter, nearly symmetric, with small round projection dorsally, deeply divided into 9–11 rays of slightly unequal length (Figure 1N), 2500–3200 µm, basal sinus ± 40°, margins distally decurved and terete in transverse section (Figure 1W), toward apices with numerous conical papillae (Figure 1X), ± 12.5 × 17.5 µm; involucre with margins hyaline or occasionally purple-tinged, with tapering ciliate lobes (Figure 1Z), 300–350 µm long, 90–150 µm wide at base, inner cells 5- or 6-sided, 52.5–75.0 × 22.5–32.5 µm, with scattered, smaller oil cells in between, cilia (1–)2–5 cells or up to 230 µm long, top cell conical, 37.5–47.5 × 10.0 µm, basally with single cell, 72.5 × 25.0 µm, but sometimes with 2; *scales of receptacle* (Figure 1S) hyaline, up to 2000 µm long and 80 µm or 6 cells wide at base, apical cell conical, ± 62.5 × 12.5 µm, following 3 cells in a vertical row, ± 57.5 × 15 µm, basal cells 62.5–87.5 × 12.5–20.0 µm, sometimes branched along the length. *Spores* 10.0–12.5 µm in diameter, triangular-globular, yellow; distal face (Figure 2A, B) with numerous highly convoluted and branched, smooth ridges; proximal face (Figure 2C, D) with faint, collapsed triradial mark, facets finely and densely granular, narrowly winged. *Elaters* yellow-brown, 350–435 × 5 µm, gradually tapering to narrow tips, bispiral. *Chromosome number*: n = 9 (Bischler-Causse 1993a).

Marchantia polymorpha, which has been known since classical times, is widespread. It has frequently been described but until recently its taxonomy has been unresolved because proper lectotypification had not been done. Amell (1963) reported it in southern Africa from Golden Gate, near Clarens in the eastern [Orange] Free State and from Zimbabwe [Southern Rhodesia], near Odnazi River Bridge, Umtali. These specimens are not held at PRE or at BOL and up to now, the presence here of *M. polymorpha* under natural conditions has not been confirmed. Bischler-Causse (1993a) stressed the need for such confirmation. It is therefore considered worthy of note that female specimens of *M. polymorpha* with cupules have recently been collected at Johannesburg Botanical Garden, Glen 3468 & 3728, in a shade house and also at Sterlig Nursery, Krugersdorp, Perold & Koekemoer CH 13640 (Figure 3). The plants are clearly introduced, but a description is nevertheless given. To complete the description and illustrations fresh male plants collected on a pavement in Ledbury, England, Perold & Koekemoer 3248, had to be used.

The specimens above have been referred to *M. polymorpha* subsp. *ruderalis* Bischl. & Boisselier-Dubayle,

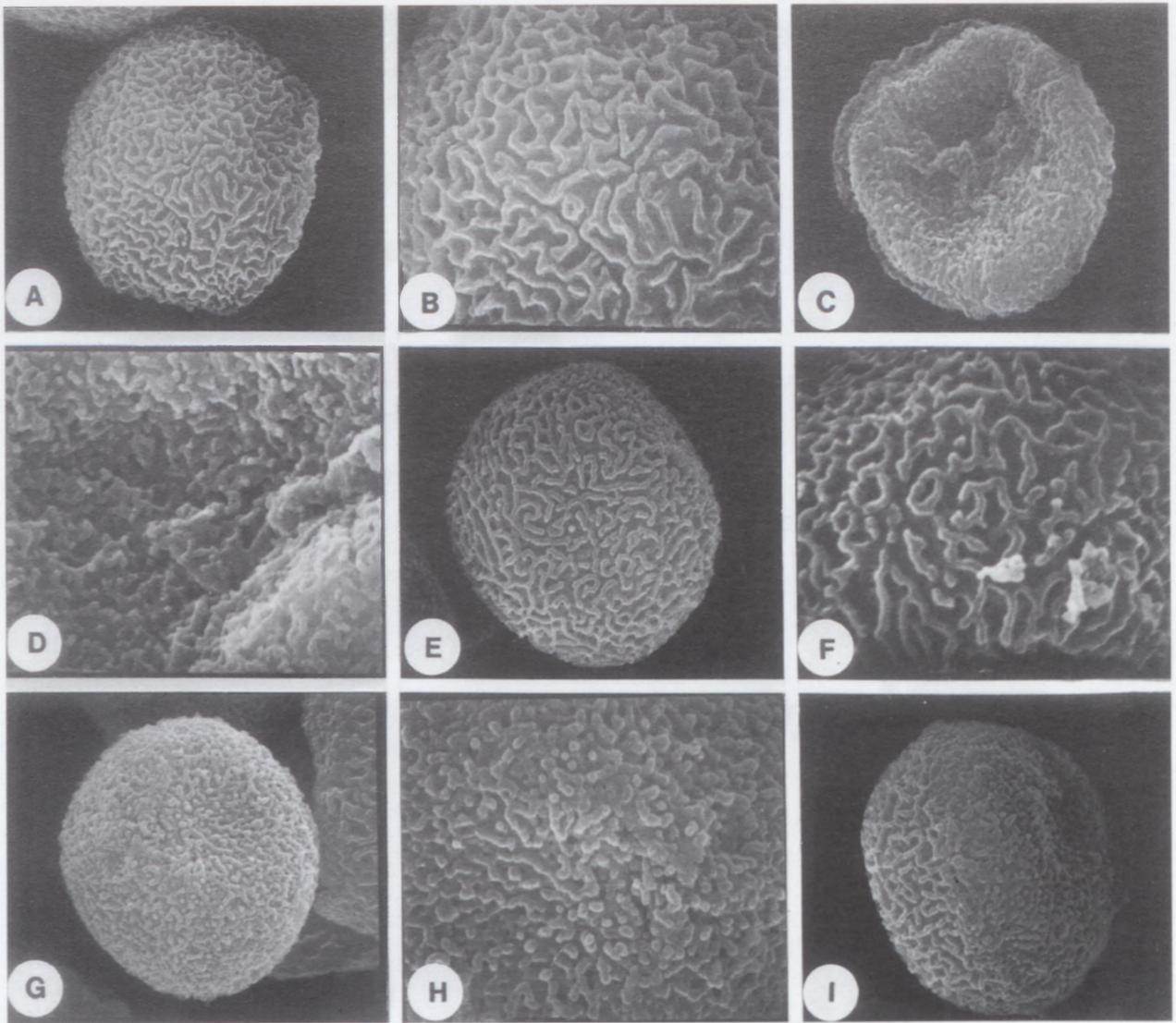


FIGURE 2.— SEM micrographs of spores. A–D, *Marchantia polymorpha*, S.M. Perold & M. Koekemoer 3248: A, distal face; B, part of distal face much enlarged; C, proximal face; D, part of proximal face much enlarged. E–I, *M. berteriana*, Geldenhuys 1332: E, distal face; F, part of distal face much enlarged; G, proximal face; H, part of proximal face much enlarged; I, side view. A, C, $\times 3006$; B, D, $\times 5780$; E, $\times 3044$; F, H, $\times 5596$; G, $\times 2875$; I, $\times 3006$.

since they grow as weeds in man-made habitats and agree in other respects with this subspecies, as distinguished by Bischler-Causse & Boisselier-Dubayle (1991). They are characterized by the fresh thalli being prostrate and bright green, with a dark, rather indistinct and discontinuous median band with elongated air chambers, by the dorsal air pores being $50.0\text{--}62.5\ \mu\text{m}$ wide, the dorsal epidermal cells $35\text{--}55\ \mu\text{m}$ long and the median scale appendages having toothed margins and being $350\text{--}500 \times 510\text{--}760\ \mu\text{m}$ in size. The other 2 subspecies of *M. polymorpha*, *polymorpha* and *montivagans*, have so far not been found in southern Africa. They are distinguished by occurring in natural habitats, with the former growing more or less erect, being dark green, with a conspicuous median dark band lacking air chambers, having small air pores, short dorsal epidermal cells and the median scale appendages having entire margins; the latter subspecies is prostrate, yellow-green, lacks a median band, the air pores are larger, the dorsal cells are of intermediate length and the median scale appendages are of average size and the margins toothed. The distinguishing characters of the subspecies are given, in case *M. polymorpha* subsp. *polymorpha* and *M. polymorpha* subsp. *montivagans* are found in southern Africa in the future.

Lectotypification of *M. polymorpha* was recently done by Bischler-Causse & Boisselier-Dubayle (1991) by means of a Dillenian illustration and by a specimen held in OXF (i.e. a typotype). This corresponds to the first of three Linnean varieties (Linnaeus 1753), namely var. [∞], which was later called '*aquatica*'. This first variety [∞] forms the basis for the application of the specific name (Isoviita 1970). However, since the lectotype of *M. polymorpha* var. *polymorpha* of Linnaeus corresponds to the taxon '*aquatica*' (at any rank), it renders that name illegitimate, because the epithet '*polymorpha*' would be used for a taxon not including its type. The best procedure seemed, therefore, for Bischler-Causse & Boisselier-Dubayle to describe their three newly separated electrophoretic groups (in three enzyme systems: esterases, peroxidases and acid phosphatases) as subspecies, give two of them new names and select good, recent type specimens. *M. polymorpha* L. subsp. *polymorpha* thus corresponds to the taxon formerly called '*aquatica*'; *M. polymorpha* L. subsp. *ruderalis* Bischl. & Boisselier-Dubayle corresponds roughly to the former *polymorpha* '*sensu stricto*' and *M. polymorpha* L. subsp. *montivagans* Bischl. & Boisselier-Dubayle roughly to the former '*alpestris*'.

On chemical evidence Markham *et al.* (1977) had previously concluded that the three taxa of *M. polymorpha* should be treated as varieties rather than as separate species, since they all possess identical flavone glucuronides.

The time of going to press of Schuster's (1992) monumental work pre-dated the publication by Bischler-Causse & Boisselier-Dubayle (1991) on the lectotypification of *M. polymorpha*, but judging by some of the remarks contained in it, it is by no means certain that he would have accepted it. He still subscribes to the genetic analyses of Burgeff (1943), although they have been shown to be out of date, and he therefore treats the segregates of *M. polymorpha* as distinct species.

As mentioned above, in southern Africa *M. polymorpha* subsp. *ruderalis* is only known from man-made sites, i.e. in nurseries. Its presence in natural habitats has not been confirmed. Asakawa *et al.* (1988) refer to the distribution of sesquiterpenoids and cyclic bis-bibenzylyls in southern African collections of *M. polymorpha*, but it is not known where the material was obtained from or who identified it. Magill & Schelpe (1979) and Arnold & De Wet (1993) list *M. polymorpha* as occurring in southern Africa, but these lists are based on erroneous information in the literature.

Marchantia polymorpha is very similar to *M. berteriana*, but can be distinguished from it by the marginal scales which are always present and which mostly extend beyond the crisped, sometimes crenulate thallus margins; by the air pores not being cruciate; by the presence of numerous papillae on the rays of the female receptacle and by the appendages of the median scales bordered by larger cells.

2. *Marchantia berteriana* Lehm. & Lindenb. in Lehm., Novarum et minus cognitarum stirpium, pugillus 6: 21 (1834); Gottsche *et al.*: 481 (1846); Steph.: 393 (1898–1900); Schiffn.: 41–44 (1896); A. Evans: 246 (1917); Hässel de Menéndez: 160 (1963); S.W. Amell: 55 (1963); E.O. Campb.: 122 (1965); Bischl.: 44 (1984); Bischl.: 81 (1989a); Bischl.: 56 (1993a). Type: 'In insula Juan Fernandez, legit cl. Bertero (Herb. Hookeri), (W8294, holo.; FH, G, NY, PC, STR, W, iso).

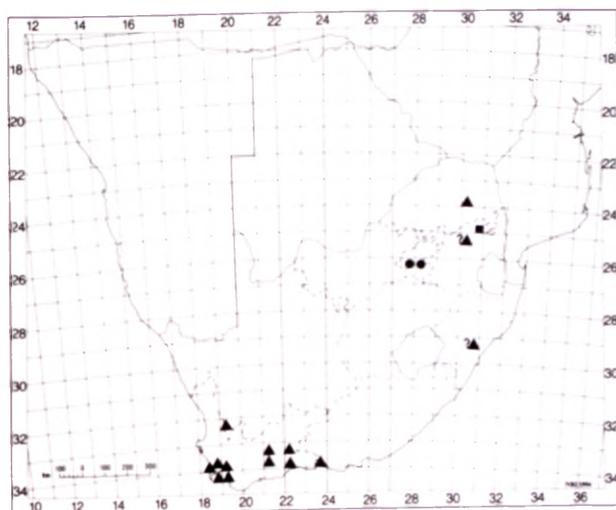


FIGURE 3.—Distribution of *M. polymorpha* var. *ruderalis*. ●: *M. berteriana*. ▲: and *M. paleacea*. ■: in southern Africa.

M. tabularis Nees: 71 (1838); Sim: 28 (1926). Type: South Africa, Tafelberg, leg. Ecklon (W8289) (female) W!, syn.; leg. Bergius (male) STR, syn.

M. contracta Bisch.: 135 (1846) (fide Bischler-Causse (1993a)). Type: South Africa, Cap. Duyvelsberg, Krauss s.n. (BM, FH, G!, PC, W).

For the rest of the synonymy consult Bischler-Causse (1993a).

Thallus robust, rather flat, almost leathery, apical segments broadly oblong (Figure 4A), green, yellowish green or bluish green and occasionally with some purple pigmentation, without distinct median band dorsally, margins hyaline, purplish or brownish, irregularly lobulate, more or less plicate but not crisped, entire or minutely crenulate, pores numerous, small, almost closed, subdorsal air chamber walls indistinct from above, when wet; thallus margins not raised or incurved, when dry; in crowded, overlying mats, repeatedly furcate but rather irregularly so. *Branches* with total length up to 80 mm, terminally up to 20 mm long and successive branches 6–10 mm apart, narrowly to moderately divergent, 9.5–12.0(–15.0) mm wide, 600–900 μm thick over midrib, laterally thinning out into wings (Figure 4C); apex notched with brownish, hyaline or partly purplish red appendages of median scales recurved over edge; margins acute, thin, slightly recurved, flanks sloping obliquely; ventral face (Figure 4B) brownish or purplish, medianly keeled, covered with rhizoids, and with 2 rows of scales on either side (sometimes with 3), extending over $\frac{3}{4}$ – $\frac{9}{10}$ of thallus width, but never right to the edge.

Dorsal epidermal cells unistratose, seldom bistratose in patches, hyaline, polygonal, 4–7-sided, (50–)57.5–77.5 \times 20.0–30.0 μm , walls slightly thickened, in transverse section 15–20 μm thick, occasionally containing an oil body; along margins (Figure 4G) 3 or 4 rows of cells, smallest in the outermost row, rectangular or polygonal, 17.5–22.5 \times 10.0–15.0 μm , enlarging inwardly, 27.5–37.5 \times 25.0–37.5 μm , air pores numerous, (107.5–)137.5–185.0 (–225.0) μm distant from each other, raised, compound, oval (37.5–)57.5–75.0 \times 27.5–47.5(–55.0) μm , encircled by (4)5–7 concentric rings of cells, 3(4) above epidermis and 3 or 4 projecting into air chambers (Figure 4F), innermost ring with collapsed cells \pm 5 μm wide, uppermost ring with 4 or 5 sausage-shaped cells, 50–55 \times 10 μm , also 4 or 5 cells in next ring, 45.0–47.5 \times 27.5–32.5 μm , those in outermost ring irregular in shape as they adjoin or partly overlie dorsal epidermal cells (Figure 4D), 55.0–62.5 \times 12.5–20.0 μm , inner opening with 4 or 5 cells, their inside walls covered with a granular deposit and strongly protuberant, leaving only a small, usually cruciate opening (Figure 4E₁, E₂). *Assimilation tissue* 45–50(–60) μm thick, $\frac{1}{10}$ – $\frac{1}{20}$ as thick as thallus, air chambers in a single layer, 77.5–120.0 μm wide, bounding walls 3 or 4 cells high, rounded or angular, 7.5–20.0 \times 10.0–12.5 μm , chambers crowded with densely chlorophyllous filaments, cells oval, round or irregularly shaped, 15.0–20.0 \times 12.5–15.0 μm ; storage tissue occupying ventral $\frac{9}{10}$ – $\frac{19}{20}$ of thickness of thallus medianly, decreasing laterally, cells angular, up to 75 μm wide, becoming smaller lower down, containing scattered starch grains and some with an oil body, sclerotic cells and mucilage cavities absent; rhizoids some smooth, \pm 27.5 μm wide, others pegged, 27.5–45.0 μm wide.

Median scales (Figure 4I) hyaline or purplish, in one row on either side of midrib, body \pm obliquely triangular, up to 1450 μm long, across base 2875–3500 μm , hardly

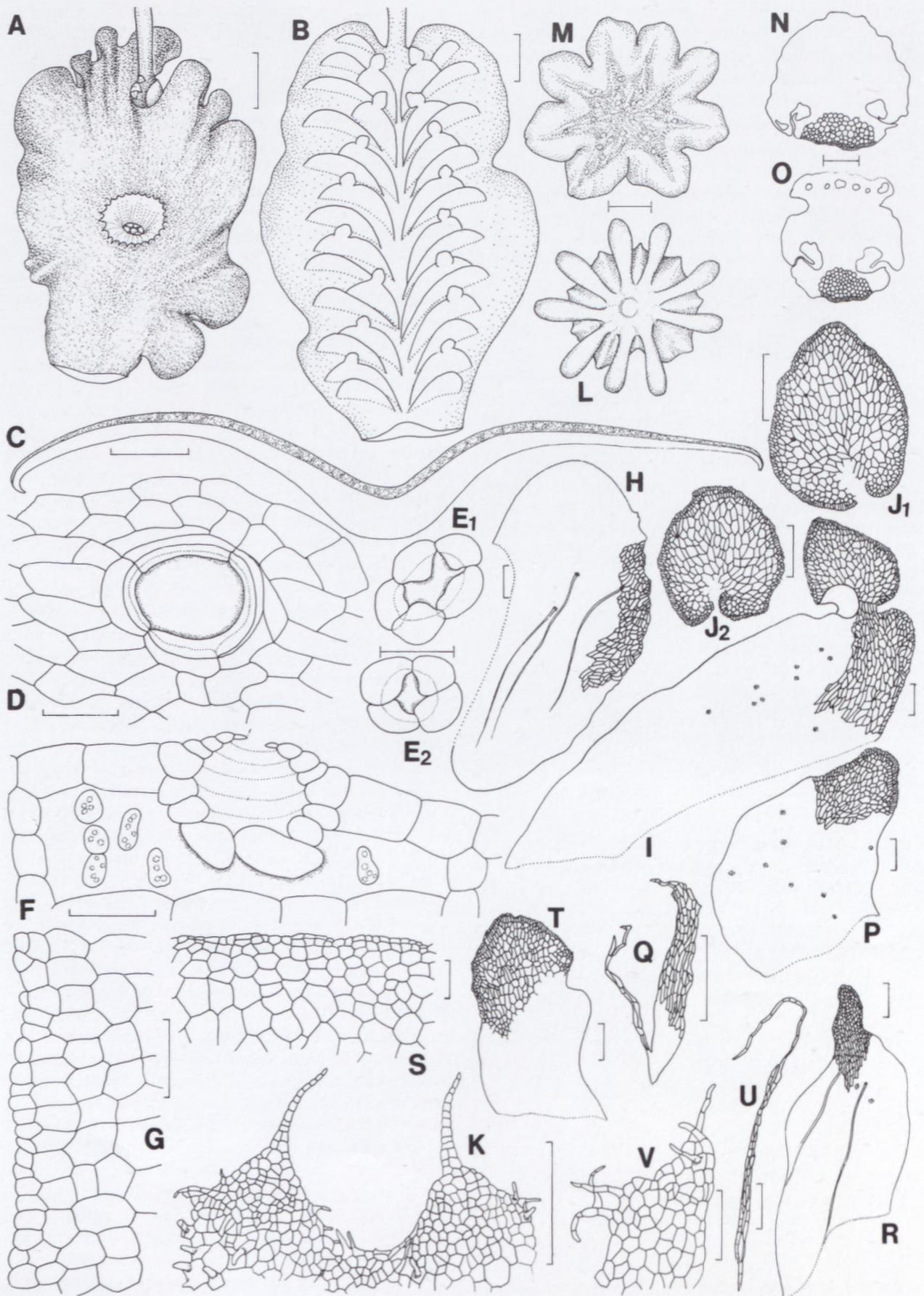


FIGURE 4.—*Marchantia berteriana* Lehm. & Lindenb. A–G, thallus: A, dorsal face of apical branch with cupule; B, ventral face of apical branch; C, t.s. of branch; D, air pore and surrounding cells from above; E₁, E₂, air pores from below; F, t.s. of air pore, dorsal epidermal cells and air chamber; G, margin. H, laminal scale; I, median scale; J₁, J₂, appendages of median scales; K, cupule margin; L, ♀ receptacle; M, ♂ receptacle; N, t.s. of ♂ stalk; O, t.s. of ♀ stalk. P–R, scale: P, from foot of ♂ stalk; Q, from along ♂ stalk; R, median scale of ♂ receptacle. S, margin of ♂ ray; T, scale from foot of ♀ stalk; U, scale from ♀ receptacle; V, margin of involucre. A, F, G, L, N, P, R, S, A.E. van Wyk 2066; B–E₁, E₂, H–J₁, J₂, M, O, T–V, Geldenhuys 1332; K, Q, Pillans 4048. Scale bars: A, B, L, M, 2 mm; C, 1 mm; D–G, 50 μm; H–K, N–R, T, 250 μm; S, U, 100 μm.

arched, central cells elongated and narrow, 4 or 5-(6)-sided, $125.0\text{--}212.5 \times 17.5\text{--}30.0 \mu\text{m}$, toward margins outer 7 or 8 rows of cells thinner-walled, orientation irregular and much smaller in size, $27.5\text{--}50.0 \times 20.0\text{--}22.5 \mu\text{m}$, with as many as 30 scattered oil cells, $\pm 87.5 \times 37.5 \mu\text{m}$, dark brown, scale gradually narrowing upwards and then $\pm 1875 \mu\text{m}$ wide, abruptly and deeply constricted at join with appendage, hyaline or purplish or both, orbicular to broadly ovate (Figure 4J₁, J₂), apex rounded to somewhat obtusely narrowed, basally cordate, $675\text{--}950 \times 650\text{--}800 \mu\text{m}$, median cells 4-6-sided, $80.0\text{--}95.0 \times 45.0\text{--}52.5 \mu\text{m}$, with 4 or 5 oil cells, margins entire or minutely crenulate, bordered by 1 or 2(3) rows of very small cells, $30.0\text{--}40.0 \times 10.0\text{--}20.0 \mu\text{m}$, mostly narrowly rectangular to subquadrate and orientated with long axis perpendicular to margin, sometimes alternating with 2 stacked cells parallel to margin, and even smaller, $12.5 \times 12.5\text{--}17.5 \mu\text{m}$. *Laminal scales* mostly hyaline, yellowish brown or reddish, lateral to, but also alternating irregularly with median scales, broadly rounded, lacking apical appendage, base flatly arched (Figure 4H), $850\text{--}1125 \times 1875\text{--}3375 \mu\text{m}$, cells in body of scale 4-6-sided, walls straight or sinuous, $92.5\text{--}125.0 \times 22.5\text{--}32.5 \mu\text{m}$, sometimes in upper part with thickened walls, but in 6 or 7 rows toward inner margins thinner-walled, smaller, $32.5\text{--}50.0 \times 12.5\text{--}25.0 \mu\text{m}$, and very variable in orientation, with ± 12 oil cells, margins entire or slightly crenulate. *Marginal scales* rarely to sometimes present, when more or less scattered and never extending beyond thallus margins, hyaline, crescent-shaped with rounded apex, $675\text{--}1250 \times 775 \mu\text{m}$, upper cells small, with thickened corners, $15.0\text{--}25.0 \times 12.5 \mu\text{m}$, inner cells with slightly sinuous walls, $35.0\text{--}58.5 \times 15.0\text{--}25.0 \mu\text{m}$, toward base cells 5- or 6-sided, up to $112.5 \times 22.5 \mu\text{m}$. *Cupule* margins with ciliate, \pm triangular lobes (Figure 4K), up to $675 \mu\text{m}$ long and $250 \mu\text{m}$ wide at base, at apex with 10 or 11 cells in a tapering, uniseriate, vertical row, top cell conical, $\pm 32.5 \times 7.5 \mu\text{m}$, lower cells larger, up to $37.5 \times 30.0 \mu\text{m}$, at base of lobes on either side a few transversely projecting (2-)3 or 4(-6)-celled cilia, lower down cupule wall several cell layers thick, exteriorly with numerous 1- or 2(-3)-celled papillae, $32.5\text{--}50.0 \times 20.0 \mu\text{m}$ and internally with many oil cells.

Dioicous. *Antheridiophore* arising from apex of terminal segment of main or short lateral branch, raised on stalk (Figure 4N), 23-30 mm long, in transverse section rounded, diameter $\pm 1000 \mu\text{m}$, cortical cells small, $10.0\text{--}15.0 \times 12.5\text{--}17.5 \mu\text{m}$, with thickened outer wall, medullary cells larger, mostly angular, $22.5\text{--}45.0 \times 15.0\text{--}45.0 \mu\text{m}$, band of air chambers absent but with 2 rhizoid furrows, $\pm 162.5 \times 100.0\text{--}125.0 \mu\text{m}$; *scales at base of stalk* large (Figure 4P), hyaline or purplish, roughly triangular or oblong, sometimes slightly bulging, lacking an appendage, up to $1200 \times 1400 \mu\text{m}$, cells in body of scale 4-6-sided, often with sinuous walls, $47.5\text{--}87.5 \times 22.4\text{--}25.0 \mu\text{m}$, along upper margins 1 or 2 rows of much smaller cells, $12.5\text{--}25.0 \times 12.5\text{--}30.0 \mu\text{m}$, with up to 10 scattered oil cells throughout; *scales along length of stalk* (Figure 4Q) hyaline, filiform, sometimes only 3 cells wide but sometimes wider and up to 9 cells wide; *receptacle* (Figure 4M) up to 10 mm in diameter, shallowly dissected into 8(9) \pm symmetric lobes, basal sinus $\pm 80^\circ$ wide; margins of lobes membranous, brownish or hyaline, minutely crenulate, with 1 or 2 rows of small cells (Figure 4S), mostly rectangular across, $15.0\text{--}20.0 \times 10.0\text{--}22.5 \mu\text{m}$, in-

ner cells larger, $52.5\text{--}87.5 \times 37.5\text{--}40.0 \mu\text{m}$; *median scales* on ventral side of lobes (Figure 4R) hyaline, $750\text{--}1375 \times 1000\text{--}1875 \mu\text{m}$, cells in body of scale 4-6-sided, up to $125 \times 50 \mu\text{m}$, thin-walled, at margins smaller, $\pm 30.0 \times 17.5 \mu\text{m}$, appendage absent or present, $\pm 267.5 \times 200.0 \mu\text{m}$, oblong, rounded apically, not or hardly constricted at join with scale, inner cells $40.0\text{--}42.5 \times 15.0\text{--}22.5 \mu\text{m}$, smaller at margins.

Archegoniophore arising from apex of terminal segment of main or short lateral branch; raised on stalk 48-65 mm long, in transverse section (Figure 4O) $1000 \times 925 \mu\text{m}$, constricted on inner side of single band of air chambers, cortical cells small, $12.5\text{--}20.0 \times 12.5\text{--}25.0 \mu\text{m}$, outer wall thicker, medullary cells angular, up to $60 \times 45 \mu\text{m}$, in between and at centre of stalk with smaller cells $\pm 25 \times 20 \mu\text{m}$, containing 2 rhizoid furrows, $\pm 240 \times 105 \mu\text{m}$; *scales at base of stalk* (Figure 4T), brownish or hyaline, without appendage, oblong or ovate, with apex rounded, large, $1575\text{--}2000 \times 800\text{--}1250 \mu\text{m}$, inner cells 4-6-sided, walls mostly straight, sometimes sinuous, $75.0\text{--}125.0 \times 27.5\text{--}42.5 \mu\text{m}$, margins apically occasionally slightly crenulate, with rectangular cells arranged at right angles to margin, small, $10.0\text{--}25.0 \times 12.5\text{--}25.0 \mu\text{m}$; *scales along length of stalk* (Figure 4U) hyaline, filiform, up to $6500 \mu\text{m}$ long, 2 or 3(4) cells wide, their average size $\pm 112.5 \times 25.0 \mu\text{m}$; *receptacle* (Figure 4L) up to 10 mm in diameter, nearly symmetric, dorsally with small round median projection, deeply divided into 9 linear rays, up to $2625 \times 550 \mu\text{m}$, basal sinus $\pm 45^\circ$ wide, margins distally slightly decurved and terete in transverse section, lacking papillae toward apex; involucre with margins hyaline or purplish, with tapering ciliate lobes (Figure 4V), base $100.0\text{--}175.0 \times 125.0\text{--}182.5 \mu\text{m}$, inner cells 5- or 6-sided, $35.0\text{--}37.5 \times 22.5\text{--}25.0 \mu\text{m}$, lower down with numerous oil bodies, up to $60.0 \times 37.5 \mu\text{m}$, each one almost filling a cell, lobes apically and at sides with numerous, tapering, branched and intertwined cilia, length up to $220 \mu\text{m}$ or 7 cells in series, $22.5\text{--}50.0 \times 20.0 \mu\text{m}$, with granules on walls of apical cells; *scales of receptacle* (Figure 4U) hyaline, filiform, up to $2150 \mu\text{m}$ long and $35.0\text{--}87.5 \mu\text{m}$ or 2-5 cells wide at base, often splitting further along and strands mostly only 2 cells wide, $80.0\text{--}87.5 \times 20.0\text{--}22.5 \mu\text{m}$, apical cell $\pm 75.0 \times 17.5 \mu\text{m}$. *Spores* $7.5\text{--}12.5 \mu\text{m}$ in diameter, \pm globular, brownish, distal face (Figure 2E, F, I) with numerous, much convoluted and branched ridges; proximal face (Figure 2G, H, I) with faint triradiate mark and winged, densely covered with numerous fine granules and tiny irregular ridges. *Elaters* yellow-brown, $(550\text{--})600\text{--}640(770) \times 5 \mu\text{m}$, gradually tapering at both ends for $150\text{--}200 \mu\text{m}$, bispiral. *Chromosome number*: $n = 9$ (Bischler-Causse 1993a).

Marchantia tabularis was described from specimens collected on Table Mountain and was placed in synonymy under *M. berteriana* by Schiffner (1896). Although Stephani (1898-1900) accepted Schiffner's decision, he still applied the epithet 'tabularis' and was followed in this by Sim (1926). Arnell (1963) gives only brief notes on *M. berteriana*. Bischler-Causse (1993a) recognized that *M. contracta*, collected by Krauss at Devil's Peak, also belongs here. *M. berteriana* is quite variable in size, but generally the plants are large. Sometimes six rows of ventral scales are present and some authors, e.g. Hässel de Menéndez (1963) and Engel (1990) recognize these as

belonging to a separate variety, namely var. *polylepida*. However, several authors (Campbell 1965; Bischler 1984) have pointed out that the number of rows of scales is too unstable to warrant the designation of a variety. Schuster (1992) has assigned *M. berteriana* to his new monotypic section, *Berteroanae*, on the absence of marginal scales, on the cruciate inner openings of the epidermal pores with six rings of cells and on the tiny marginal cells of the median scale appendages. Bischler-Causse (1993c) is, however, not convinced that this splitting is necessary, since marginal scales are fairly frequently present and the pores are often similar to those in other species of subgenus *Marchantia*.

Marchantia berteriana generally grows on damp soil, and sometimes on wet rocks, at stream banks, near waterfalls, along paths, in kloofs, passes, ravines, gorges, in forests under trees or in burnt-over areas.

It is widely distributed in the southern hemisphere, from South America, south to the Antarctic Peninsula and north to Costa Rica, islands of the Atlantic and south Indian Ocean, southern Africa, Australia, Tasmania, New Zealand, New Guinea, New Caledonia, Java and Sulawesi (Bischler-Causse 1993a). In southern Africa (Figure 3) it is known from the Western Cape, which has winter rain, and from Kwazulu-Natal as well as the Northern Province [Northern Transvaal] which have summer rain. Exact localities of two of these collections by Wilms and by MacLea are not known. This distribution indicates that the species seems to be indifferent to the seasonality of the rainfall, in contrast to several other members of the Marchantiales which are \pm restricted to either winter or summer rainfall areas.

Of the 50 specimens examined 36% had cupules, 34% had antheridiophores and 46% archegoniophores; only 6% had both.

Specimens of *M. berteriana* are easily distinguished by the tiny marginal cells of the median scale appendages, by the cruciate dorsal pores and by the lobulate thallus margins. The membranous margins of the rays of the male receptacle also have very small cells. Otherwise it is quite similar to *M. polymorpha*, except for the latter having papillae on the rays of the carpocephalum. The ornamentation of their spores is also quite similar.

Subgenus **Chlamidium** (Corda) Bischl., Cryptogamie, Bryologie et Lichénologie 3: 362 (1982); Bischl.: 89 (1989a); Bischl.: 65 (1993a).

Marchantia L. sect. *Chlamidium* (Corda) Nees: 60, 101 (1838). Type: *Chlamidium indicum* Corda (Sieber flora mart. exsicc. No. 375) = *Marchantia chenopoda* L. Type: Sieber 378 p.p. (W. neo.; STR, iso., fide Bischl. 1984).

Thallus branches rather narrow, from 2.4 to \pm 10.0 mm wide, rarely more, margins nearly flat, entire, sometimes slightly undulate, rarely crisped. *Dorsal epidermis* without papillae; air pores surrounded by (4–)5–7 concentric rings of cells, at inner openings with straight or convex walls, rarely with pronounced, rounded processes, and pores then cruciate; storage tissue often with scattered

sclerotic cells. *Scales* in 4 rows, covering $1/4$ to $2/3$ of ventral face, with oil cells present or absent, median scales with appendages variously shaped, orbicular, ovate or triangular, apically often acuminate, acute or apiculate, seldom rounded; margins entire, crenulate-serrate, coarsely toothed or lobed; laminal scales as long as, or longer than wide, sometimes in 2 incomplete rows on either side of median scales, apically acute or obtuse, with papillae, upper cell walls lacking trigones. *Cupules* with margins ciliate, almost entire, or with ciliate lobes, externally without, or rarely with papillae.

Dioicous. *Antheridiophores* with receptacle symmetric or asymmetric, palmate or rarely peltate, rays shallowly or deeply dissected; stalks with 2(–4) rhizoid furrows, air chambers in a single band or absent. *Archegoniophores* with receptacle symmetric, or sometimes asymmetric; dissected into 5–9 rays, flat or convex but never terete; scales of receptacle in African species apically with marginal cells rectangular and long axis parallel to margins; involucre margins ciliate or crenulate to entire, rarely with ciliate lobes; stalks with 2–4 rhizoid furrows, air chambers in 1 or 2 bands. *Spores* larger than in subgenus *Marchantia*, 20–35 μ m in diameter; ornamentation on distal face generally with thick ridges separated by dense granules; on proximal face with coarse granules only, triradiate mark and thick wing usually present.

Subgenus *Chlamidium* contains three sections, *Paleaceae*, *Chlamidium* and *Papillatae*. Section *Paleaceae* contains a single species. Sections *Chlamidium* and *Papillatae* are each represented in southern Africa by a single species.

Marchantia section **Paleaceae** Bischl. in Bryophytorum Bibliotheca 38: 90 (1989a); Bischl.: 67 (1993a). Type species: *M. paleacea* Bertol. [lecto. fide Grolle: 210 (1976)].

Thallus with branches (3.5–)6.0–8.0(–11.0) mm wide, irregularly spaced, narrowly divergent. *Dorsal epidermis* without papillae; air pores with inner opening cruciate, inside walls of bordering cells strongly protuberant. *Median scales* with appendage oblong, ovate or suborbicular, apically rounded, acute or shortly apiculate, basally cordate, width across broadest part 650–750 μ m, margins entire, crenulate or slightly denticulate; with 1, 2 or more oil cells. *Cupules* with margins triangularly lobed and ciliate, externally with 1- or 2-celled papillae.

Dioicous. *Antheridiophore* on stalk lacking band of air chambers and basally surrounded by large scales without an appendage; receptacle peltate, shallowly dissected into 6–10 broad, rounded lobes, dorsal surface without papillae. *Archegoniophore* on stalk having a single band of small air chambers, basally surrounded by large scales, their apices rounded, rarely with a short appendage; receptacle bearing prominent median projection dorsally, deeply divided into 8 or more convex lobes, basally costate, apically truncate or hardly broadened, emarginate; involucre margin with ciliate lobes. *Spores* 19–24 μ m in diameter, ornamentation on distal face lacking areolae, mostly covered with a rather featureless, granular layer or with very irregular ridges, broken up or folded in or convoluted; proximal face different, thickly winged, triradiate

mark faint, covered with dense granules or centrally with narrow, irregular granular ridges. Only *M. paleacea* belongs to this section. The ornamentation of its spores is distinctive. It also differs from the other two sections in subgenus *Chlamidium*, by the shape of the female receptacle and by the ciliate, lobed margins of the involucre and the cupules.

3. *Marchantia paleacea* Bertol., *Opuscoli scientifici di Bologna* 1: 242 (1817); Bischl.: 55 (1984); Bischl.: 91 (1989a); Bischl.: 68 (1993a) subsp. **paleacea**. Type: Italy, Borgonuovo secus valles in Liguria orientali, *D. Turio*, 1810 [BOLO, lecto, fide Grolle (1976)].

M. papillata Raddi var. *italica* Raddi: 20 (1822). Syntypes: Italy, Contorni di Firenze, *Raddi s.n.* (BOLO, FH, FI, G, PC, STR).

For the rest of the synonymy see Bischler-Causse (1993a).

Thallus medium-sized to large, firm and occasionally somewhat leathery, apical segments oblong (Figure 5A), bright green to slightly bluish green, sometimes blotched with dark red pigmentation, generally lacking but now and then with faint, short stretches of dark median band dorsally, margins mostly deep red or pink, entire, proximally, however, undulate and scalloped, pores numerous, small, generally closed, subdorsal air chamber walls visible from above and these flecked with numerous white oil bodies, when wet; thallus margins \pm crinkled, not raised or incurved, when dry; in crowded, overlying mats, repeatedly furcate. *Branches* with total length up to 45 mm, terminally up to 15 mm long and successive branches rarely more than 10 mm, but mostly less apart, narrowly divergent, (3.5–)6.0–8.0(–11.0) mm wide, 750–800 μ m thick over midrib, laterally thinning out into wings (Figure 5C), apex notched with dark red to marginally orange appendages of median scales recurved over edge; margins acute, thin, flanks sloping obliquely; ventral face (Figure 5B) dark red entirely or only medianly, and the remainder green, with 2 rows of scales on either side of ventral keel, extending over $1/3$ – $1/2$ of thallus width.

Dorsal epidermal cells mostly unistratose, here and there bistratose, hyaline, long-rectangular or polygonal, (45.0–)60.0–80.0 \times 27.5–37.5 μ m, walls thin or slightly thickened, in transverse section 20.0–27.5 μ m thick, oil bodies usually subdermal, almost filling cell, \pm 32.5 \times 30.0–40.0 μ m, dark brown, globular to subglobular; along margins (Figure 5G) mostly with 3 rows of cells, narrowest in outermost row, long rectangular, 17.5–37.5 \pm 5.0 μ m, in next row 4- to 6-sided, 30.0–35.0 \times \pm 12.5 μ m, and in innermost row 30.0–52.5 \times 17.5–27.5 μ m; air pores numerous, 192.5–262.5 μ m distant from each other, raised, compound, oval, 40.0–50.0 \times 35.0–42.5 μ m, encircled by 4–6(–7) concentric rings of cells, 2 or 3 above epidermis and up to 4 projecting into air chambers (Figure 5F), innermost ring with collapsed cells, \pm 5 μ m wide, uppermost ring with (3)4 or 5 cells, 37.5–62.5 \times 7.5 μ m, cells in next ring 37.5–42.5 \times 7.5–12.5 μ m and in outer ring, sometimes up to six, 42.5–62.5 \times 15.0–22.5 μ m (Figure 5D), inner opening with 4 or 5 cells, inside walls mostly with granular deposit and strongly protuberant, leaving only a small cruciate opening (Figure 5E₁, E₂). *Assimilation tissue* 75.0–100.0 μ m thick, $1/10$ – $1/8$ as thick as thallus, air chambers in a single layer, 112.5–187.5 μ m wide, bounding walls 3 or 4(5) cells high, 22.5–35.0 \times

20.0–27.5 μ m, crowded with chlorophyllose filaments, cells mostly irregularly shaped, 17.5–27.5 \times 12.5–20.0 μ m; storage tissue occupying ventral $7/8$ – $9/10$ of thickness of thallus medianly, decreasing laterally, cells angular, crowded together, 52.5–67.5 μ m wide, walls pitted, central area sometimes stained purple, sclerotic cells and mucilage cavities absent in specimens seen, but reportedly sometimes present; rhizoids mostly smooth, 17.5–27.5 μ m wide, occasionally pegged, 10.0–17.5 μ m wide.

Median scales (Figure 5I) mauve, in one row on either side of midrib, body \pm obliquely triangular, up to 1050 μ m long, base arched and continuing into long 'tail', when up to 3250 μ m wide, inner cells elongated, 4–6-sided, 52.5–87.5 \times 20.0–25.0 μ m, walls straight or somewhat sinuous toward margin, cells in outer 8 or 9 rows with thinner, often sinuous walls, orientation very irregular and smaller in size, 15.0–55.0 \times 12.5–20.0 μ m, sometimes 3 or 4 marginal cells grouped together and slightly raised in a little peak from centre of which 1 or 2 slender papillae project, scattered throughout up to 25 oil cells, \pm 37.5 \times 27.5 μ m, oil body almost filling cell, scale gradually narrowing upwards and then \pm 750 μ m wide, abruptly deeply constricted at join with appendage (Figure 5J₁, J₂), marginally orange-brown or purplish, internally pink or occasionally hyaline, ovate, oblong or suborbicular, apically rounded, acute or shortly apiculate, basally cordate, rarely with small basal lobe, 810–875 \times 650–750 μ m, inner cells 5- or 6-sided, 65.0–77.5 \times 37.5–52.5 μ m, with 1, 2 or more oil cells or even none; margins entire, crenulate or slightly denticulate, bordered by 1 row of smaller cells, quadrate to rectangular, sometimes walls sinuose, 17.5–37.5 \times 10.0–27.5 μ m, orientated parallel to or perpendicular or oblique to margin, sometimes partly protruding, submarginal cells \pm 62.5 \times 27.5 μ m. *Laminal scales* (Figure 5H₁, H₂) mauve or internally mauve and externally hyaline, in one row on either side of and lateral to, but alternating irregularly with median scales, \pm oblong, but not quite symmetric, base slightly arched or oblique, 750–1575 \times 500–650 μ m, cells in body of scale elongated, 4–6-sided, walls straight or sinuose, 55.0–100.0 \times 17.5–27.5 μ m, with up to 10 scattered oil cells, toward margins cells smaller, 17.5–32.5 \times 15.0–25.0 μ m, their orientation very variable, a few along inner sloping margin grouped together and forming individual little peaks from tips of which slender papillae project. *Cupule* margins (Figure 5K) with ciliate, \pm triangular lobes, 380–420 μ m long and 200–240 μ m wide at base, apically up to 6 cells in a tapering, uniseriate, vertical row, top cell conical, 25.0–32.5 \times 15.0–20.0 μ m, lower cells, 20.0–40.0 \times 20.0–25.0 μ m, base of lobes broadened to 6–9 adjacent cells, 4- or 5-sided, 27.5–35.0 \times 22.5–27.5 μ m, from margins of lobes on both sides, horizontally projecting, 1–3(4)-celled cilia, lower down cupule wall several cell layers thick, exteriorly with 1- or 2-celled papillae, up to 37.5 μ m long, and internally with numerous oil cells.

Dioicous. *Antheridiophore* not seen as none available for study. *Archegoniophore* arising from apex of terminal segment of main or short lateral branches, raised on stalk, 10–11 mm long, partly reddish, in transverse section (Figure 5N), 750 \times 700 μ m, cortical cells small, 15.0–25.0 \times 12.5–27.5 μ m, outer wall thicker, medullary cells rounded, 42.5–45.0 \times 35.0–42.5 μ m, smaller cells in between and at centre of stalk, 12.5–22.5 \times 20.0–25.0 μ m, with single

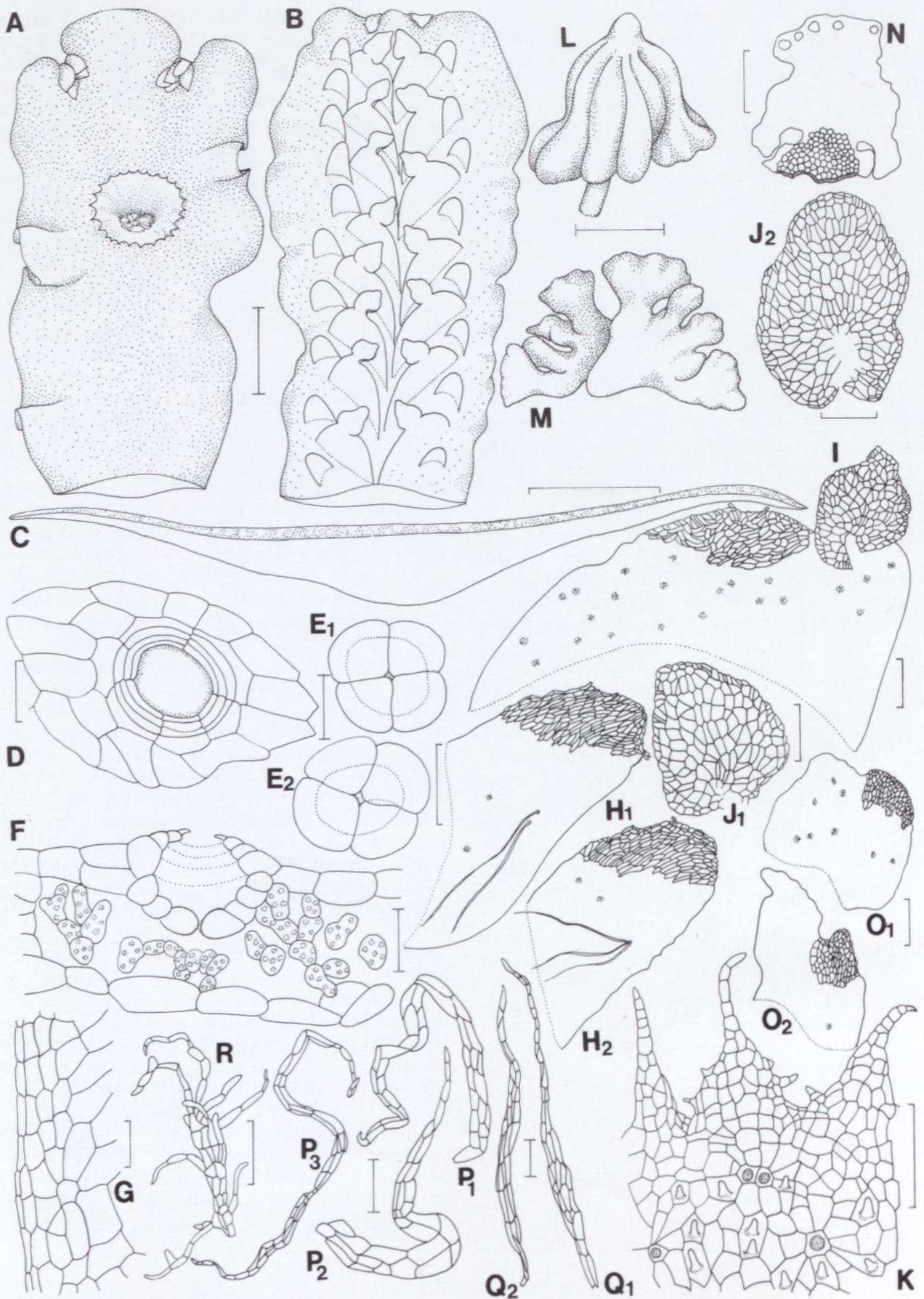


FIGURE 5.—*Marchantia paleacea* Bertol. A–G, thallus: A, dorsal face of apical branch; B, ventral face of apical branch; C, t.s. of branch; D, air pore and surrounding cells from above; E₁, E₂, air pores from below; F, t.s. of air pore, dorsal epidermal cells and air chamber; G, margin. H₁, H₂, laminal scales; I, median scale; J₁, J₂, appendages of median scales; K, cupule margin; L, ♀ receptacle from above; M, ♀ receptacle from side; N, t.s. of ♀ stalk. O–Q, scale: O₁, O₂, from foot of ♀ stalk; P₁–P₃, from along ♀ stalk; Q₁, Q₂, from ♀ receptacle. R, margin of involucre. A, E₁, E₂, G, I, J₁, J₂, Rankin 206; B–D, F, H₁, H₂, K, S.M. Perold 3264; L–R, C. Tavares LISU P 66716. Scale bars: A, B, L, M, 2 mm; C, 1 mm; D–G, 50 µm; H–K, N–R, 250 µm.

band of 4 small air chambers, $\pm 62.5 \times 30.0 \mu\text{m}$, and 2 rhizoid furrows, lined with purple-walled cells, $\pm 112.5 \times 72.5 \mu\text{m}$, *scales at base of stalk* (Figure 5O₁, O₂) conspicuous, brown, rounded or partly 2-lobed or irregularly shaped, often bulging, without or with short apical appendage, $1025\text{--}1150 \times 900\text{--}1750 \mu\text{m}$, inner cells 5- or 6-sided, $52.5\text{--}70.0 \times 25.0\text{--}32.5 \mu\text{m}$, with up to ± 10 oil cells, $30 \times 20 \mu\text{m}$, margins \pm entire, cells quadrate or rectangular or irregularly shaped, $22.5\text{--}47.5 \times 15.0\text{--}20.0 \mu\text{m}$, long axis orientated parallel or perpendicular to margins; *scales along length of stalk* (Figure 5P₁–P₃) hyaline or purplish, filiform, up to $1750 \mu\text{m}$ long, toward apex ± 4 single cells in a row, $67.5\text{--}75.0 \times 10.0\text{--}20.0 \mu\text{m}$, lower down 3 or 4 cells wide, $75.0\text{--}132.5 \times 20.0\text{--}22.5 \mu\text{m}$; *receptacle* (Figure 5L, M) ± 4 mm in diameter, nearly symmetric, dorsally with prominent median projection, deeply divided into 8 lobes, up to $750 \mu\text{m}$ long, narrow at base and some of them wider at \pm truncate apex, basal sinus $\pm 100^\circ$ wide; involucre with margins (Figure 5R) hyaline or purplish, divided into narrow lobes $\pm 500 \times 90 \mu\text{m}$, fringed with cilia $180\text{--}650 \mu\text{m}$ long, which consist of several cells in a uniseriate row, apical cell $\pm 75 \times 25 \mu\text{m}$, lower cells $82.5\text{--}92.5 \times 20.0\text{--}30.0 \mu\text{m}$, toward base often with 1 or 2 serially arranged transverse cells on one or both sides, originating at join between 2 successive cells; *scales of receptacle* (Figure 5Q₁, Q₂) hyaline or purplish, filiform, up to $2075 \mu\text{m}$ long, apically cells in a uniseriate row, $62.5\text{--}85.0 \times 12.5\text{--}22.5 \mu\text{m}$, then 2 cells and eventually 4 cells wide, up to $92.5 \times 25.0 \mu\text{m}$. *Spores* and *elaters* not available for study. *Chromosome number*: $n = 9$ (Bischler 1984, 1988, 1989a).

Marchantia paleacea has been known since the time of Micheli (1729), who described and illustrated it; but it was not accepted by Linnaeus (1753). After *M. polymorpha*, it was to become only the second species in the genus to be recognized from Europe, and was described by Bertolini (1817) from material collected in Italy.

It has been placed in subgenus *Chlamidium* on account of the four rows of ventral scales which are restricted to the median part of the thallus. It is assigned to the monotypic section *Paleaceae* because of the shape of the female receptacle, the structure of the margins of the involucre and the cupules, which have ciliate lobes (Bischler-Causse 1993a) with papillae externally.

The species has a circumtethyan distribution, ranging from the southern states of the USA, Mexico and Central America, to the Mediterranean, the Caucasus, the Himalayas, and to the Far East (Bischler 1988). In Africa (and the neighbouring islands), it is known from Algeria, Ethiopia, the Azores, Terceira and Réunion. Bischler-Causse (1993a) states that its presence on the Canary Islands, Madeira and in Morocco needs confirmation. A specimen from Madeira, *Tavares* (LISU) was seen by me, and its archegoniophores were studied and are illustrated in Figure 5L–R. The presence of *M. paleacea* on Madeira is thus confirmed. Bischler-Causse (1993a) thought that the single specimen, *Rankin 206* (BM), from the vicinity of Pilgrim's Rest, South Africa, that she had seen, might have been mislabelled. A computer printout at PRE, however, revealed that several other bryophytes were collected by Rankin in the same area, with collecting numbers both lower and higher than the one referred to, so that it was

unlikely to have been mislabelled. I have recently also collected it near Pilgrim's Rest (Figure 3) on a steep earth bank of the Blyde River, where it grew down to the water's edge together with *M. debilis*. The plants were sterile unfortunately, as was Rankin's collection, but both had cupules. As noted above, archegoniophores from Madeira were used for the description and illustrations, but no antheridiophores were available for study.

In the Far East a subspecies, *M. paleacea* subsp. *dip-tera* (Nees & Mont.) Hatt., is recognized (Bischler-Causse 1989a). It is distinguished from subsp. *paleacea* by the epidermal pores of the thallus usually being surrounded by 7 or 8 rings of cells, by the frequent presence of non-functional female receptacles and by the marginal cells of the median scale appendage having the long axis oblique to perpendicular to the margins (not parallel to).

Marchantia paleacea subsp. *paleacea* is regarded as morphologically stable and can be distinguished from the other species of subgenus *Chlamidium* by its cruciate epidermal pores and its cupules which have margins with ciliate lobes. The appendage of the median scales is ovate to orbicular. Schuster (1992) regards *M. berteriana* as the closest ally to *M. paleacea*, because it also has cruciate epidermal pores and its cupules have margins with triangular lobes bearing teeth (or cilia) as well. *M. berteriana* is however, classified in subgenus *Marchantia*.

Marchantia section Chlamidium

Thallus with branches (6.0–)7.0–8.5 (–10.0) mm wide, generally rather remotely spaced and narrowly divergent. *Dorsal epidermis* without papillae; air pores with inner opening bordered by cells, their inside walls convex to nearly straight or with short, rounded processes. *Median scales* with appendage ovate to orbicular or broadly triangular, apically rarely obtuse, mostly acute, sometimes shortly apiculate, basally rounded or cordate, width across broadest part $375\text{--}530 \mu\text{m}$, margins entire or sometimes bluntly toothed; with 1 or 2 oil cells, rarely more numerous. *Cupules* with ciliate margins, cilia up to 6 or 7 cells long and 3 cells wide basally, exteriorly sometimes also with several cilia.

Dioicous. *Antheridiophore* on stalk which mostly lacks bands of air chambers but with 2 or 3 rhizoid furrows; basally surrounded by quite large scales, often with an appendage; receptacle palmate, shallowly to deeply dissected into 6–8(–10) rays, dorsal surface with or without papillae. *Archegoniophore* on stalk having 2 bands of air chambers and 2 rhizoid furrows; basally surrounded by quite large scales, often with an appendage and rather similar to median scales of thallus; receptacle with or without small, median projection dorsally, shortly divided into 9–11 rather flat lobes, sometimes basally narrow, widening slightly toward truncate apex; involucre margins shortly to long ciliate. *Spores* $20\text{--}30 \mu\text{m}$ in diameter, ornamentation on distal face with wide, irregular, smooth ridges forming incomplete areolae filled with nodules; proximal face entirely covered with nodules.

Of the southern African taxa, only *M. pappeana* belongs in this section. The ornamentation of its spores is

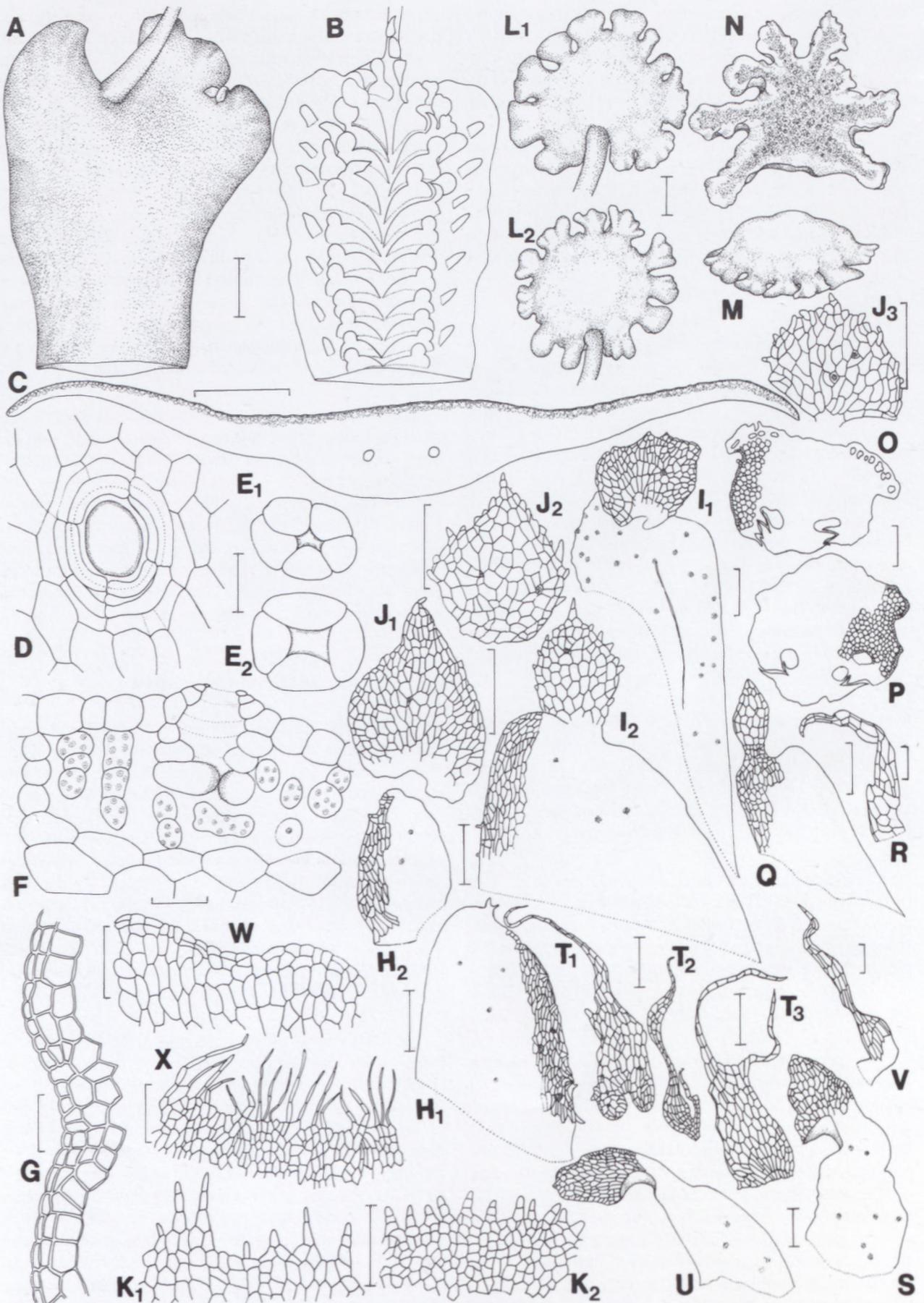


FIGURE 6.—*Marchantia pappeana* Lehm. subsp. *pappeana*. A–G, thallus. A, B, apical branch: A, dorsal face; B, ventral face. C, t.s. of branch. D–F, air pore from above; E₁, E₂, from below; F, t.s. of dorsal epidermal cells and part of air chamber. G, margin. H–J, scales: H₁, H₂, laminal; I₁, I₂, median; J₁–J₃, appendages of median scales. K₁, K₂, margins of cupules; L–Q, receptacles: L₁, L₂, ♀ from above; M, ♀ from side; N, ♂; O, t.s. of ♀ stalk; P, t.s. of ♂ stalk; Q, median scale of ♂. R–V, scales: R, along ♂ stalk; S, foot of ♂ stalk; T₁–T₃, ♀ receptacle; U, foot of ♀ stalk; V, along ♀ stalk. W, margin of ♂ ray; X, margin of involucre. A, G, H₁, I₂, J₂, K₁, L₁, L₂, M, T₁–T₃, X, *Koekemoer 1050*; B, C, F, J₃, K₂, N, *Perold & Koekemoer 2918*; D, O, V, *Burgoyne 2068*; E₁, S, *H. Anderson 1261*; E₂, I₁, J₁, H₂, *Perold & Koekemoer 2841*; P–R, W, *Hilliard & Burt 15460*; U, *H. Anderson CH13278*. Scale bars: A, B, L–M, 2 mm; C, 1 mm; D–G, 50 µm; H–V, X, 250 µm; W, 100 µm.

referred to as the *chenopoda* type; there are, however, two other spore coat ornamentation types in the section (Bischler-Causse 1989a). The section is distinct in the shape of the female receptacle and in the ciliate margins of the involucre and cupules.

4. *Marchantia pappeana* Lehm. in *Novarum et minus cognitarum stirpium*, Pugillus X: 21 (1857); Bischl.: 76 (1993a). Type: South Africa, 'In Prom. B. S. leg. Pappe', ex herb. Lehmann (RO, holo.?: G! ex herb. Univ. di Roma).

M. pappeana subsp. *pappeana* Bischl.: 82 (1993a).

M. flavescens Steph. in *Bonner*: 107 (1953). Type: Fernando Pó, 1911 *Mildbraed* 6275 (G).

M. parviloba Steph.: 305 (1895); Vanden Berghen: 46 (1954); S.W. Arnell: 56 (1963). Type: Uganda, Runssoro, um 2 800 m, 10 Juli 1891, *Stuhlmann* 2368a (G, lecto, fide Vanden Berghen: 46 (1954); BM, isolecto, fide Bischl.: 82 (1993a)).

M. planiloba Steph.: 90 (1886); Henriques: '153, 154'; 181, 182 ('1886', 1887). Type: São Tomé, Cachoeira do Rio Manuel Jorge, circa S. Nicolau, 800 m, 1885, *Moller* 32 [G, lecto, fide Vanden Berghen: 52 (1960)].

M. planiloba Steph. var. *walteri* Burgeff: 276 (1943). Type: Tanzania, 'Nderema in Ost-Usambara, etwa 1 000 m, leg. H. Walter', syn. fide Bischl.: 83 (1993a).

M. stephanii Vanden Berghen: 50 (1954) [= *M. umbellata* Steph.: 305 (1895), nom. illeg.]. Type: Tanzania, Usambara, *Holst* 692 (FH, G), syn. fide Bischl.: 83 (1993a).

M. wilmsii Steph.: 126 (1892). Type: South Africa, Transvaal, *McLea* in *Rehmann Hep. austro-afri. exs. 1* [PC, lecto, fide Vanden Berghen: 44 (1954); BM!, G, NY, S, isolecto, fide Bischl.: 84 (1993a)].

M. winkleri Steph. in *Bonner*: 112 (1953). Type: Cameroon, *Winkler* 270 (G).

Thallus medium-sized to large, rather distantly and irregularly branched, not ribbon-like or flat, apical segments oblong to obovate, light green to yellowish green, often purplish pink or deeply purple toward margins, or irregularly smudged with purple on dorsal surface, without dark median band (Figure 6A), margins undulate, scalloped, usually hyaline, occasionally purple, entire, mostly crisped; pores quite large and subdorsal air chamber walls visible from above and flecked with whitish oil cells, when wet; thallus margins rarely raised, not incurved when dry; in densely crowded and irregularly overlying mats. *Branches* with total length up to 50 mm, terminally 10–15 mm long and successive branches generally 10–13 mm apart, mostly narrowly to moderately divergent, (6.0–)7.0–8.5 (–10.0) mm wide, 740–925 µm thick over midrib, laterally thinning out into wings (Figure 6C); apex notched, with appendages of purple-brown median scales recurved over edge (Figure 6A); margins acute, thin; flanks sloping obliquely; ventral face medianly keeled, with rows of purple scales on either side, extending over 40–75% of thallus width (Figure 6B).

Dorsal epidermal cells unistratose, very rarely bistratose in patches, hyaline, mostly 5- or 6-sided (Figure 6D), 42.5–80.0(–105.0) × 22.5–37.5 µm, thin-walled, not thickened at corners, rarely containing an oil body, in transverse section 25.0–32.5 µm thick; along margins 1–2(3) rows of cells, mostly narrowly rectangular (Figure 6G), 22.5–30.0 × 10.0–17.5 µm, sometimes shorter than broad, ± 17.5 × 35.0 µm, innermost third row of cells larger, 27.5–32.5 × 27.5 µm; air pores fairly numerous, dis-

tance between them (200–)325–575 µm, raised, compound, oval or round, (65–)90–105 × 70–100 µm, surrounded by 6 or 7 concentric rings of cells, 3 or 4 above epidermis and 2 or 3 projecting into air chambers (Figure 6F), innermost ring of upper cells, ± 50.0 × 7.5 µm, next 2 rows of cells ± 40.0 × 7.5–10.0 µm, partly overlying the outer, larger ring of 7 or 8 polygonal cells, up to 75.0 × 17.5 µm, inner opening with 4 or 5(6) bulging cells (Figure (6E₁, E₂), 30.0–42.5 × 12.5–15.0 µm, inner walls convex or almost straight, densely covered by dark granules. *Assimilation tissue* 60–90 µm thick, ¹/₁₂–¹/₈ as thick as thallus medianly, air chambers in a single layer, with 2 or 3 cells in vertical bounding walls, 27.5–42.5 × 17.5–30.0 µm, occasionally containing an oil body, ± 35 µm in diameter, air chambers 275–387 µm wide, crowded with chlorophyllose filaments (Figure 6F), 1–3-celled, often irregular in shape, 20.0–30.0 × 15.0–17.5 µm; storage tissue occupying ventral ⁷/₈–¹¹/₁₂ of thickness of thallus medianly, decreasing laterally, often with a wide, upper, central, purple-stained band, cells angular, closely packed, 25–50 µm wide, rather smaller below, but much larger laterally, sclerotic cells present or absent, mucilage openings few, up to 200 µm wide, or absent; rhizoids some smooth, width 15–45 µm, others pegged, 10–15 µm wide.

Median scales (Figure 6I₁, I₂) purple, in one row on either side of midrib, body obliquely triangular, 800–1125 µm high, 1430–1875 µm wide across arched base, mostly ending below in a long 'tail', central cells elongated, 5- or 6-sided, walls often sinuous, 92.5–107.5 × 30.0–37.5 µm, smaller toward margins and longer and narrower in 'tail', oil bodies scattered, margins sometimes with protruding papillae, ± 50.0 × 12.5 µm, scale narrowing upwards, deeply constricted where joined with appendage (Figure 6J₁–J₃), purple brown or reddish, ovate to orbicular or broadly triangular, apically rarely obtuse, mostly acute, sometimes shortly apiculate, 520–550 × 375–530 µm, apiculus with a vertical row of 2 or 3 cells, 35.0–62.5 × 20.0–27.5 µm, basally rounded or cordate, margins entire or sometimes bluntly toothed, teeth 32.5–50.0 × 20.0–30.0 µm, marginal cells 50.0–62.5 × 17.5–37.5 µm, only slightly smaller than inner cells, 4–7-sided, 75.0–87.5 × 32.5–42.5 µm, oil cells solitary, rarely more numerous. *Laminal scales* (Figure 6H₁, H₂) mauve with hyaline base, in one row at lateral sides of median scales, obtusely triangular, (750–)980–1125 × (360–)630–1075 µm, cells 4–7-sided, 45.0–70.0 × 20.0–27.5 µm, smaller toward margins, oil cells scattered, appendage lacking, margins often with protruding papillae. *Cupules* with margins ciliate (Figure 6K₁, K₂), cilia (122.5–)180.0–315.0 µm or up to 6(7) cells long, top cell 45.0–67.5 × 15.0 µm, lower cells 30.0–75.0 × (17.5–)22.5–32.5 µm, basal cells ± 50.0 × 62.5 µm, sometimes 2 adjoining, ± 75.0 × 17.5–30.0 µm, exterior surface occasionally also ciliated.

Dioicous. *Antheridiophore* arising mostly from apex of terminal segment of main branch, raised on stalk, 9–18(–32) mm long, diameter 775–925 µm, in transverse section (Figure 6P) with one row of small cortical cells, (12.5–)15.0–20.0 × (12.5–)15.0–17.0 µm, outer wall slightly thickened, medullary cells larger, up to 60 µm wide, but in between with smaller cells, ± 20 µm wide, air chambers mostly absent, with 2(3) rhizoid furrows, ± 150 µm wide; *scales at base of stalk* (Figure 6S), 1 or 2, hyaline, broadly triangular, 1000–1150 × 550–750 µm,

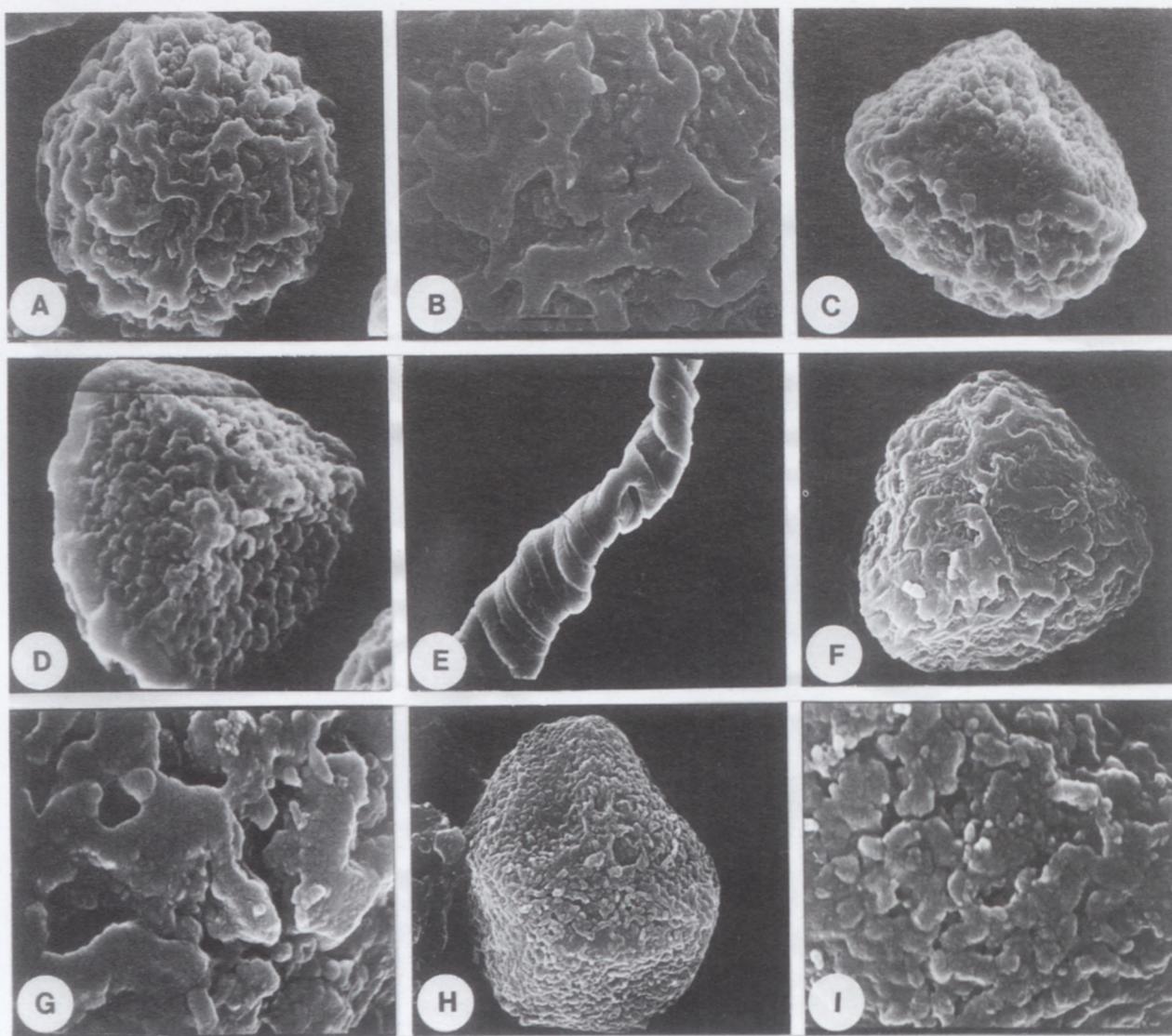


FIGURE 7.—SEM micrographs of spores. A–E, *Marchantia pappeana*, H. Anderson CH13278: A, distal face; B, part of distal face much enlarged; C, side view; D, proximal face. E, part of elater, much enlarged. F–I, *M. debilis*, Preuss s.n.: F, distal face; G, part of distal face much enlarged; H, proximal face; I, part of proximal face, much enlarged. A, $\times 1233$; B, $\times 2340$; C, D, $\times 1200$; E, $\times 740$; F, $\times 1412$; G, I, $\times 5148$; H, $\times 1373$.

sometimes with appendage, $\pm 675 \times 500 \mu\text{m}$, partly or not constricted at base, cells $75\text{--}80 \times 30\text{--}55 \mu\text{m}$, slightly smaller lower down; *scales along length of stalk* (Figure 6R), narrowly triangular and tapering toward apex, up to $1300 \mu\text{m}$ long, base $\pm 175 \mu\text{m}$ wide, cells $62.5\text{--}100.0 \times 27.5\text{--}37.5 \mu\text{m}$; *receptacle* 9–14 mm in diameter, palmate, divided into 6–8 rays (Figure 6N), 1.7–3.4 mm long, $\pm 3.5 \text{ mm}$ wide, basal sinus $120^\circ\text{--}140^\circ$, margins of rays reddish, undulating, entire (Figure 6W), outer cells long and narrow, $\pm 27.5 \times 10.0 \mu\text{m}$, here and there alternating with wider cells, $25.0\text{--}37.5 \times 25.0 \mu\text{m}$; *median scales* on ventral side of rays brownish, obtusely triangular, body $\pm 750 \times 500 \mu\text{m}$, cells $55\text{--}75 \times 25 \mu\text{m}$, mostly with appendage tapering to acute apex (Figure 6Q), $350\text{--}375 \times 125\text{--}250 \mu\text{m}$, cells $\pm 62.5 \times 37.5 \mu\text{m}$.

Archegoniophore generally arising from apex of terminal segment of main branch, raised on stalk, 16–32(–60) mm long, diameter 850–1050 μm , wider across chambers, $\pm 1250 \mu\text{m}$, in transverse section (Figure 6O) with one row of small, rounded, cortical cells, $15.0\text{--}25.0 \times 12.5\text{--}25.0 \mu\text{m}$, outer wall slightly thickened, medullary cells angular, $\pm 50 \mu\text{m}$ wide, with smaller, $\pm 20 \mu\text{m}$ wide cells in between, air chambers in 2 separate and opposite

bands $\pm 500 \mu\text{m}$ wide, containing several small air chambers, $\pm 62 \mu\text{m}$ high, also with 2 rhizoid furrows, $\pm 85 \times 195 \mu\text{m}$; *scales at base of stalk*, 1 or 2 present (Figure 6U), larger, $\pm 1350 \times 850 \mu\text{m}$, shape irregular, cells $87.5\text{--}107.5 \times 25.0 \mu\text{m}$, often with \pm triangular appendage, slightly constricted at base or hardly so, $750\text{--}900 \times 500\text{--}550 \mu\text{m}$, cells $92.5\text{--}137.5 \times 25.0\text{--}37.5 \mu\text{m}$, 4–7-sided, walls straight, shorter along margin, $37.5\text{--}42.5 \times 37.5\text{--}50.0 \mu\text{m}$; *scales along length of stalk* (Figure 6V), hyaline strands, $1300\text{--}1950 \times 70\text{--}200 \mu\text{m}$, tapering, apically filamentous; *receptacle* (6.5–)8.0–11.0 mm in diameter, sometimes with small, rounded, median projection dorsally, shortly and \pm symmetrically divided into 9–11 lobes (Figure 6L₁, L₂, M) (occasionally 1 or 2 lobes replaced by male rays), 1.4–1.7 mm long, base narrow, 1.0–1.25 mm, widening to 2.1–3.0 mm, toward truncate apex, basal sinus $\pm 30^\circ$; margins of involucre hyaline, ciliate (Figure 6X), cilia delicate, sometimes collapsed, $187.5\text{--}200.0 \mu\text{m}$ long, consisting of cells, $62.5\text{--}100.0 \times 17.5\text{--}25.0 \mu\text{m}$, occasionally base broader, up to $37.5 \mu\text{m}$ wide, inner cells angular, $50.0\text{--}62.5 \times 32.5 \mu\text{m}$, with numerous large oil bodies; *scales of receptacle* mauve or hyaline, tapering toward apex, sometimes abruptly so, occasionally forked (Figure 6T₁–T₃), up to $3250 \times 250 \mu\text{m}$,

cells 4–7-sided, 75.0–137.5 × 37.5–40.0 µm, filamentous apices ± 450 µm long, with apical cell conical, ± 50 × 15 µm, lower cells ± 65 × 30 µm, several oil cells present, ± 50.0 × 32.5 µm, and marginally with unicellular papillae, ± 37.5 × 15.0 µm. *Spores* 22.5–30.0 µm in diameter, triangular-globular, yellow-brown, distal face (Figure 7A, B) with irregular, ± smooth ridges, forming incomplete areolae filled with nodules; proximal face (Figure 7C, D) with faint triradiate ridge, each facet densely covered with nodules, some discrete, others confluent, narrowly winged, margin entire. *Elaters* yellow-brown, up to 825 × 7.5 µm, tapering toward ends, 5.0 µm wide, bispiral (Figure 7E). *Chromosome number*: n = 18 (Bischler-Causse 1993a).

Although *M. pappeana* had already been described by Lehmann in 1857 and was mentioned by Stephani (1898–1900), the name has been neglected by subsequent authors and specimens in most herbaria, including PRE, are labelled as *M. parviloba*, *M. planiloba* or *M. wilmsii*. The species is listed as *M. parviloba* in Magill & Schelpe (1979). Several authors had suspected, however, that *M. parviloba* was synonymous with *M. planiloba* (Vanden Berghen 1965; Jones & Harrington 1983). Bischler-Causse (1993a) found that only seven of the 18 specimens cited by Stephani, belong to *M. pappeana* and of the 30 kept in his herbarium, only 11 belong here.

Arnell (1963) mistakenly considered *M. pappeana* to be a synonym of *M. berteriana*. He may, however, have been misled by a specimen in S (where Lehmann's original collections are kept) which was labelled *M. pappeana*, but actually contains *M. berteriana*, as was shown by Bischler-Causse (1993a). Arnell (1963) merely surmised that *M. parviloba* would be found in the northern parts of South Africa, but he had probably only seen specimens from Zaïre [Congo], Tanzania [Tanganyika] and Zimbabwe [Southern Rhodesia].

Marchantia pappeana often grows in the same localities as *M. debilis*, on vertical soil banks of streams, at waterfalls, at sluice canals, very rarely on rotting wood or on rocks, in open grassland or in forests, sometimes in deep shade.

It is widely distributed in tropical Africa, Bischler-Causse (1993a) reporting it from the Cape Verde Islands to Ethiopia and south to southern Africa, generally at an altitudinal range of 1 000–2 500 m. In southern Africa (Figure 8) it is known from the Northern Province [Northern Transvaal] and Eastern Transvaal, Gauteng [PWV], Swaziland, Kwazulu-Natal, eastern [Orange] Free State and Lesotho. It has also been collected at Kirstenbosch Botanical Garden a number of times and the type specimen is from Promontorium Bonae Spei.

Of the 50 specimens examined, 62% had cupules, 20% had antheridiophores and 34% had archegoniophores; only 6% had both. Morphologically the species is variable, exhibiting this trait even among specimens from the same geographical area. Generally, however, it can be distinguished by being larger than *M. debilis* and by lacking a dark median line on the dorsal surface of the thallus; its median scale appendages are large and often marginally toothed, with the inner cells large, presenting a 'loose' appearance; its cupules have longer cilia; the female re-

ceptacle is shortly divided into rays and the involucre margin is ciliate; androgynous branches in the female receptacle are sometimes present.

Marchantia pappeana subsp. *pappeana* is distinguished from *M. pappeana* subsp. *robusta*, a close relative in South India and Sri Lanka, by the latter having numerous sclerotic cells and mucilage cavities in the thallus; oil bodies in the median scale appendages are, however, absent.

Marchantia section Papillatae Bischl. in Cryptogamie, Bryologie et Lichénologie 10: 69 (1989); Bischl.: 99 (1993a). Type: *M. papillata* Raddi (PI, lecto., Bischl.: 95 (1984).

Thallus with branches rather narrow, (2.1)–4.5–7.3 mm wide, ribbon-like, often quite regularly spaced, moderately to widely divergent. *Dorsal epidermis* without papillae; air pores with inner opening bordered by cells, their inside walls convex or straight. *Median scales* with appendage orbicular or ovate, apically acute or apiculate, seldom obtuse, basally rounded, width across widest part 275–340 µm, margins toothed; oil cells absent. *Cupule* margins with short cilia, 3(4) cells long and 1 or 2 cells wide basally, external surface without papillae.

Dioicous. *Antheridiophore* on stalk without or with 1 or 2 bands of much reduced air chambers and 2 rhizoid furrows, basally surrounded by smaller, narrowly triangular scales, sometimes divided above into filamentous segments; receptacle smallish, palmate, asymmetric and deeply divided into (4)–5–7 rays, dorsal surface without papillae. *Archegoniophore* on stalk with single band of air chambers (in African taxon) and 2 rhizoid furrows; basally surrounded by smaller, ± triangular scales, gradually tapering to filiform apex; receptacle smallish, with a rounded median projection dorsally, deeply divided into 8–10 lobes, basally convex and costate, apically broadened; involucre margins entire or crenulate. *Spores* 25–32 µm in diameter, ornamentation on distal face with irregular coarse ridges, forming incomplete areolae filled with granules; proximal face densely verrucose.

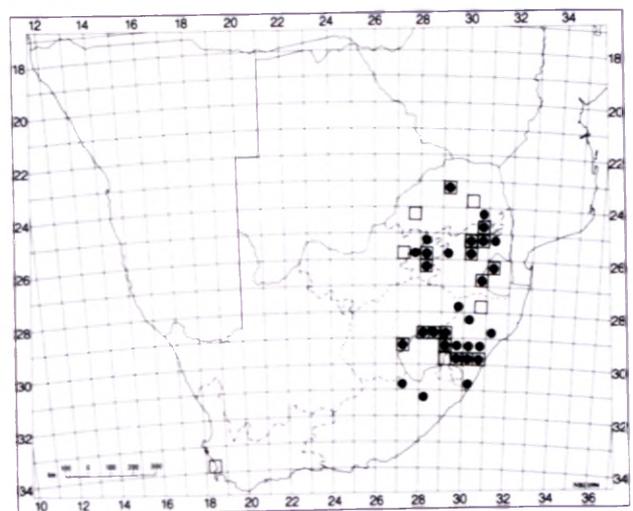


FIGURE 8.—Distribution of *M. pappeana* var. *pappeana*, □, and *M. debilis*, ●, in southern Africa.

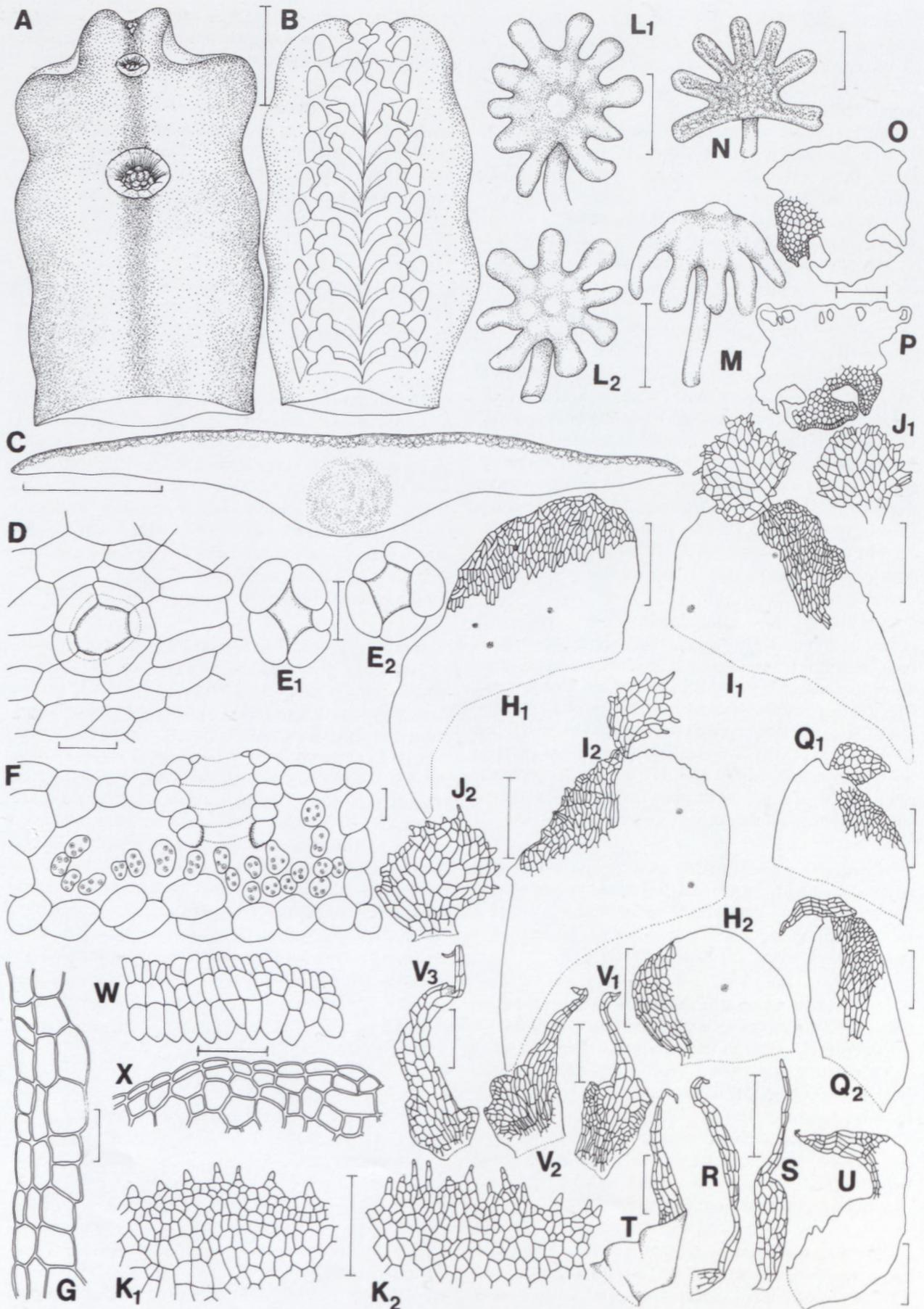


FIGURE 9.—*Marchantia debilis* Goebel. A–G, thallus. A, B, apical branch: A, dorsal face, with cupules; B, ventral face. C, t.s. of branch; D–F, air pore: D, from above; E₁, E₂, from below; F, t.s. of dorsal epidermal cells and air chamber. G, margin. H₁, H₂, laminal scales; I₁, I₂, median scales; J₁, J₂, appendages of median scales; K₁, K₂, margins of cupules. L–Q, receptacles: L₁, L₂, ♀ from above; M, ♀ from side; N, ♂, O, t.s. of ♂ stalk; P, t.s. of ♀ stalk; Q₁, Q₂, median scales of ♂ ray. R–V, scale: R, along ♂ stalk; S, along ♀ stalk; T, base of ♀ stalk; U, base of ♂ stalk; V₁–V₃, ♀ receptacle. W, margin of ♂ ray; X, margin of involucre. A, *H. Anderson* CH1223; B, R, U, W, X, *Mogg* 6172; C–G, H₂, J₁, K₁, *Condy* 90; H₁, I₁, I₂, K₂, *Bester* 2544; J₂, *Glen* 1940; L₁, L₂, M, P, S, T, *Dieterlen* 850; N, *Sim* CH1345; O, *S.M. Perold* 2891; Q₁, Q₂, V₁–V₃, *S.M. Perold* 3048. Scale bars: A–B, L–N, 2 mm; C, 1 mm; D–G, 50 μm; H–K₂, O–V₃, 250 μm; W, X, 100 μm.

Only *M. debilis* of the southern African taxa belongs to this section. Bischler-Causse (1993a) states that it is closest to the Asiatic species, *M. emarginata* subsp. *tosana*. The ornamentation of the spores is of the *papillata* type. The section differs from sect. *Paleaceae* and sect. *Chlamidium* in the shape of the female receptacle, with the lobes costate basally and broadened apically.

5. *Marchantia debilis* Goebel in Organographie der Pflanzen. 1. Bryophyten 2, edn 2: 901 (1915); Bischl.: 100 (1993a). Type: Cameroon, Urwaldgebiet von Bipindi, Zenker, *Flora von Kamerun* exs. 1339 (BM!, BR, E, F, G, GOET, M, S, iso.).

M. chevalieri Steph. in Bonner: 103 (1953). Type: Ivory Coast, Haute Côte d'Ivoire, pays Djola, environs de Ona, 4-1909. *Chevalier* s.n. (G, PC).

Thallus smallish to medium-sized, rather flat and ribbon-like, apical segments oblong or broadly lingulate, green or occasionally purplish all over, when much exposed to bright sun, usually with a narrow, dark, broken, longitudinal median band dorsally (Figure 9A), margins narrowly reddish purple or hyaline, entire; pores quite small, subdorsal air chamber walls visible from above, when wet; thallus margins not raised or incurved, sometimes with slight longitudinal indentation along midline and apex occasionally incurved, when dry; in crowded, overlying patches or occasionally in partial rosettes, up to 75 mm across, repeatedly pseudodichotomously furcate, often rather regularly. *Branches* with total length up to \pm 38 mm, terminally 5–12 mm long and successive branches 5–7(–9) mm apart, mostly moderately to widely divergent, 4.5–7.3 mm wide, 675–850 μ m thick over midrib, laterally thinning out into wings (Figure 9C); apex notched, with appendages of several reddish brown or purplish median scales recurved over edge; margins acute, thin, occasionally slightly crisped, flanks sloping obliquely; ventral face medianly keeled and densely covered with long strands of rhizoids, on either side with rows of purple scales extending over 70% or more of thallus width (Figure 9B).

Dorsal epidermal cells unistratose, rarely bistratose in patches, mostly hyaline, polygonal, (4)–5–7-sided, 37.0–62.5 \times 22.0–32.0 μ m, thin-walled, not thickened at corners, in transverse section \pm 17.5 μ m thick, occasionally containing a round oil body, \pm 37.5 μ m in diameter, along margin 2 rows of narrow, \pm rectangular cells, (10.0)–20.0–30.0(–37.5) \times (7.5)–12.5–17.5 μ m (Figure 9G), innermost third row of cells mostly larger, 30.0–37.5 \times 15.0–22.5 μ m; air pores quite numerous, (100)–215–275(–475) μ m distant from each other, raised, compound, oval, 37.5–62.5 \times 40.0–52.5 μ m, surrounded by (4)5 or 6 concentric rings of cells (Figure 9D), 2 or 3 above epidermis and 2 or 3 projecting into air chambers (Figure 9F), innermost ring of upper cells \pm 7.5 μ m wide, cells of middle ring \pm 12.5 μ m wide and outermost ring with 6 or 7 larger cells, 35.0–62.5 \times 17.5–22.5 μ m, somewhat variable in shape and partly overlying epidermal cells, inner opening (Figure 9E₁, E₂) with 4 or 5 rather swollen cells, 20–25 \times 35–42 μ m, their inside walls \pm convex or nearly straight. *Assimilation tissue* up to 150 μ m thick, \pm $\frac{1}{6}$ as thick as thallus, air chambers in a single layer (Figure 9F), (105)–150–300 μ m wide, cells in bounding walls \pm 32.5 \times 17.5 μ m, crowded with densely

chlorophyllose, mostly 3-celled filaments, cells \pm 20 \times 15–25 μ m; storage tissue occupying ventral $\frac{5}{6}$ of thickness of thallus medianly, decreasing laterally, cells angular, medianly \pm 50 μ m wide, compact, much enlarged laterally, sclerotic cells and mucilage cavities usually absent; rhizoids some smooth, 12.5–25.0 μ m, others pegged, 5.0–12.5 μ m wide.

Median scales (Figure 9I₁, I₂) brownish or purplish, in one row on either side of midrib, body \pm obliquely triangular, up to 625 μ m long, base slightly arched, its width up to 3000 μ m, central cells 4–6-sided, walls often sinuous, 65.0–87.5 \times 17.5–27.5 μ m, elongating and narrowing into long 'tail', (100.0)–137.5–182.5 \times 12.5–17.5 μ m, oil bodies scattered, upper margins of scale serrate, as it narrows and becomes constricted where joined with appendage (Figure 9J₁, J₂), mauve generally, orbicular or ovate, apically acute or apiculate, rarely rounded, 350–375 \times 275–340 μ m, median cells 67.5–75.0 \times 30.0–37.5 μ m, smaller at toothed margin, \pm 42.5 \times 25.0 μ m, teeth conical, 1-celled, \pm 37.5 \times 20.0, or 2-celled, 45.0–62.5 \times 15.0–42.5 μ m, oil bodies absent. *Laminal scales* (Figure 9H₁, H₂) brownish, in one row on lateral sides of median scales, \pm ovate, rounded apically, lacking appendage, 450–560 \times 430–670(–900) μ m, sometimes with short 'tail' (Figure 9H₁), cells (50.0)–58.5–67.5 \times 17.5–25.0 μ m, walls often sinuous, oil bodies rare or absent, sometimes with marginal papillae, 50.0 \times 12.5 μ m. *Cupules* with margins shortly ciliate (Figure 9K₁, K₂), some cilia unicellular, others 3 cells and up to 75 μ m long, apical cells conical, 20–30 \times 15 μ m, basally 1 or 2 cells wide.

Dioicous. *Antheridiophore* arising from apex of terminal segment of main branch or of short lateral branch, on stalk (2.5)–7.0–16.0 mm long, diameter 625–700 μ m, in transverse section (Figure 9O) with 1 row of cortical cells, 17.5–22.5 \times 10.0–17.5 μ m, outer wall curved, medullary cells angular, many up to 50 μ m wide, but in between smaller cells, only 17.5 μ m wide, air chambers much reduced, in single band, rhizoid furrows 2, \pm 160 μ m wide; *scales at base of stalk* (Figure 9U), narrowly triangular, 750–1250 μ m long and 150–500 μ m wide at base, sometimes \pm midway divided into (2)3 segments, only central part elongated and tapering to filamentous apical string of \pm 5 single cells, top cell \pm 30 \times 10 μ m, basal one \pm 45.0 \times 27.5 μ m, cells in body of scale \pm 92.5 \times 27.5 μ m, margin with a few papillae, 37.5 \times 7.5 μ m; *scales along length of stalk* filiform (Figure 9R), up to 1100 \times 50 μ m, 2 or 3 cells wide, except for apical row of up to 5 single cells, and sometimes basally with short cellular strands at sides of long main one; receptacle 7.5–9.0 mm in diameter, asymmetric, above without antheridial papillae, divided into (4)5–7 rays (Figure 9N), 1.5–3.0 mm long and \pm 1.2 mm wide at base, narrowing slightly to tip, basal sinus \pm 130°, margins undulating, entire (Figure 9W), hyaline, cells in 1 or 2 rows, rectangular, 17.5–32.5 \times 10.0–25.0 μ m; median scales on ventral side of rays (Figure 9Q₁, Q₂) hyaline or mauve, obtusely triangular, up to 1000 \times 670 μ m, cells 4–6-sided, 35.0–62.5(–100.0) \times 20.0–27.5 μ m, at margin with some papillae, sometimes with an apical appendage, constricted at its base or not, narrowly to broadly triangular, 300–430–x 100–200 μ m, brownish with mauve cell walls, cells 50–60 \times 25–35 μ m, smaller toward apex, 20 \times 15–22 μ m.

Archegoniophore at apex of terminal segment of main branch or of short lateral branch, raised on stalk, 9–16 mm long, diameter 400–550 μm , in transverse section (Figure 9P) with 1 row of cortical cells, $\pm 12.5 \times 22.5 \mu\text{m}$, medullary cells 22–40 \times 15–30 μm , with 2 rhizoid furrows, $\pm 75 \times 130 \mu\text{m}$, and mostly a single band of air chambers, the latter up to 85.0 \times 37.5 μm each, rarely 2 bands or a split band present; *scale(s) at base of stalk* (Figure 9T), brownish, \pm triangular, 900–1000 \times 400–450 μm , apex filiform with 3 or 4 single cells in a row, $\pm 32.5 \times 12.5 \mu\text{m}$, then widening gradually below, upper cells thick-walled, 50.0–55.0 \times 27.5–37.5 μm , thinner-walled below, sometimes with short appendage at the side; *scales along length of stalk* (Figure 9S) scattered, $\pm 700 \times 112 \mu\text{m}$, narrowing above to $\pm 35 \mu\text{m}$ wide, cells $\pm 75 \times 15 \mu\text{m}$; *receptacle* (3.5)–4.5–7.0(9.0) mm in diameter, dorsally with a rounded projection medianly (Figure 9L₁, L₂, M) and deeply divided into 8–10 lobes, 0.8–1.25 mm long, narrower at base and widening toward apex, basal sinus 40°–60°; margins of involucre hyaline, entire or crenulate, cells rectangular across to 5-sided (Figure 9X), 15.0–22.5 \times 27.5–37.5 μm ; *scales of receptacle* (Figure 9V₁–V₃) hyaline or yellow-brown or purple, 800–1000 \times 330–370 μm , irregularly shaped, cells 75.0–100.0 \times 37.5–42.5 μm , 5- or 6-sided, thick-walled, at basal margin smaller, $\pm 32.5 \times 15.0 \mu\text{m}$, thin-walled and sinuous, at apex 3 cells in a row, top cell conical, 40–75 \times 10–12 μm , gradually widening lower down and sometimes with filiform appendage at the side. *Spores* 25.0–32.5 μm in diameter, faintly triangular-globular, brown, distal face (Figure 7F, G) with irregular, coarse ridges, forming incomplete areolae, spaces between filled with granules; proximal face (Figure 7H, I) with triradiate mark hardly visible, facets densely verrucose. *Elaters* brown, up to 295 \times $\pm 7.5 \mu\text{m}$, bispiral. *Chromosome number*: $n = 9$ (Bischler-Causse unpublished).

Bischler-Causse (1993a) states that this species, which is confined to Africa, has not been mentioned since its description by Goebel (1915) and that it occurs in various herbaria under 14 different names, but most commonly under *M. wilmsii*, *M. planiloba* and *M. chevalieri*. She also remarked that most authors considered *M. chevalieri* to be a synonym of *M. wilmsii*, but the lectotype of *M. wilmsii* (McLea!, syntype of Rehmann exsiccate) selected by Vanden Berghen (1954), belongs to *M. pappeana* and is an unfortunate choice.

The syntypes of *M. wilmsii* cited by Stephani are *McLea in Rehmann Hep. austro-afr. exs. 1* and 'Prope Lydenburg et Greytown Dr Wilms'. Bischler-Causse (1993a) states that the McLea specimens are male and correspond to *M. pappeana*; the Wilms specimens from Lydenburg are female with cupules, or are sterile and also belong to *M. pappeana*, whereas the Greytown specimens are male with cupules and contain *M. debilis*. Bischler-Causse (1993a) concludes that Stephani probably had *M. pappeana* in mind, and not *M. debilis*, since he clearly described *M. pappeana* under the epithet *M. wilmsii*. In Stephani's herbarium, she found that 13 of the 16 '*M. wilmsii*' specimens belong to *M. pappeana* and only three to *M. debilis*.

It is indeed fortunate that Bischler, with her long and intimate experience with *Marchantia* species, was able to

resolve the taxonomy of this species, since neither Vanden Berghen (1954, 1965), nor Arnell (1963) nor Jones & Harrington (1983) managed to do so. Jones & Harrington (1983) regarded '*M. wilmsii*' as the commonest *Marchantia* species in tropical Africa and readily recognizable by the presence of the dark dorsal line. Specimens held at PRE, that belong here, were mostly identified as *M. wilmsii*. The species is also listed as such in Magill & Schelpe (1979) and in Arnold & De Wet (1993).

Marchantia debilis generally grows on damp soil on vertical stream banks or waterfalls, on mud (or occasionally on stones) of stream beds, at weirs, or sluice canals, on stone dam walls kept wet by spray, and on soil overlying sandstone or granite, in open grassland or in forests, sometimes in partial shade.

It is widely distributed in Africa, Bischler-Causse (1993b) stating it to occur from Morocco to South Africa, as well as on Réunion and also in the eastern part of Madagascar. In southern Africa (Figure 8) it occurs in the summer rainfall areas of the Northern Province [Northern Transvaal] and Eastern Transvaal, Gauteng [PWV], Swaziland, Kwazulu-Natal, eastern [Orange] Free State, Lesotho and Eastern Cape.

Most of the 98 specimens examined had cupules, but only 10% had antheridiophores and 16% had archegoniophores; 3% had both.

Sterile plants of *M. debilis* can be distinguished from *M. pappeana*, the species it has frequently been confused with, by the smaller size of the rather ribbon-like thallus, by the dark median line on the dorsal face of the thallus, by the smaller appendages of the median scales and by the shortly ciliate or almost entire margins of the cupules. Fertile plants should present no problem to identify as the smallish male and female receptacles, the latter with deeply divided lobes, are quite distinctive and the margin of the involucre is entire.

ACKNOWLEDGEMENTS

I wish to sincerely thank Dr H. Bischler-Causse for refereeing this paper and for her helpful suggestions; the curators of BM, BOL, BR, G, LISU and W for the loan of specimens; my colleagues at NBI for collecting specimens; the artist, Mrs M. Steyn; the typist, Mrs J. Mulvenna, and the photographer, Mrs A. Romanowski, for their valued contributions.

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SPECIMENS EXAMINED

H. Anderson 1223 (5), CH4497 (5), CH4501 (4), CH13278 (4), CH13279 (5) PRE. S.W. Arnell 1058 (2) BOL. (sub *M. tabularis*); 1075 (2) BOL.; 1234 (5) BOL.

Barnard CH 1315 (sub *M. tabularis*) (2) PRE. Bester 2544 (5) PRE. Bews CH1321 (sub *M. tabularis*) (2), CH1348 (5) PRE. Bingham 8181

(5) (Zambia) PRE. Bolus CH1319 (sub *M. tabularis*) (2) PRE. Bosman CH195 (5) PRE. Bottomley CH1335 (sub *M. wilmsii*) (4) PRE. Breutel s.n. (2) W. Burgovne 1588, 2068 (4) PRE. Burt Davy 435 (5) PRE.

Child 26211 (2) BOL. Cholnoky 929 (sub *M. wilmsii*) (4) PRE. Condy 90 (5), CH13638 (4) PRE.

Dieterlen 850 (sub *M. polymorpha*) (5) PRE. *Doidge CH54* (2) PRE. *Drège s.n.*, 8286 (2) W. *Duthie CH1320* (sub *M. tabularis*) (2) PRE.

Ecklon 8284, 8289 W; *G546*, *G2072/7G* (typus) (2) G. *Edwards CH1346* (sub *M. wilmsii*) (4) PRE. *Esterhuysen 34979a* (2) BOL. *Eyles CH1311* (sub *M. tabularis*) (2) PRE.

Garside 6186 (2) PRE. *Geldenhuis 1061*, 1332 (2) PRE. *Germishuizen 4411*, 6031 (5) PRE. *Gerstner 583* (5) PRE. *Glen 1690*, 1940, 2189, 2207 pp. (5) PRE; 2207 pp. (4) PRE; 3007 (5) PRE; 3009, 3012, 3125a (4) PRE; 3468, 3728 (1) PRE. *Guthrie 52555* (2) BOL.

Hepburn CH1223, *CH1343* (5) PRE. *Hilliard & Burt 15460* (sub *M. wilmsii*) (4) BOL.

Kluge 2442 (5) PRE. *Koekemoer 1049* (5), 1050 (4) PRE. *Krauss 8291* (sub *M. contracta*) (2) G.

Lambert 7 (5) PRE. *Lanham 72* (sub *M. polymorpha*) (4) PRE. *Leendertz 755c* (sub *M. polymorpha*) (5) PRE. *Lübenau-Nestlé SA269* (5) PRE.

McLea in Rehmann exs. 1 (sub *M. wilmsii*) (4) BM. *Marais (Duthie 5163)* (sub *M. wilmsii*) (4) BOL. *Mogg CH159* (2) PRE; *CH1193*, *CH4150*, 4227, 6172 (5) PRE. *Moonsammy 17 (NH 16194)* (sub *M. wilmsii*) (4) PRE. *Morley 298* (2) PRE.

Oliver 54680 (2) BOL. *Onderstall 314* (5) PRE.

Pappe s.n. (typus) (4) G. RO. *Pattison 14479* (2) BOL. *J.J. Perold, CH13644* (4) PRE. *S.M. Perold, 41*, 154, 164, 166, 168, 245, 1073 (5) PRE; 2500 (4) PRE; 2549 (2) PRE; 2675 (Malawi), 2701, 2891 (5) PRE; 2926 (4) PRE; 2945, 3048, 3239, 3245 (5) PRE; 3246, 3250, 3251 (4) PRE; 3252 (5) PRE; 3260a (4) PRE; 3261–3263 (5) PRE; 3264, 3265 (3) PRE; 3266 (5) PRE; 3267, 3268 (4) PRE. *Perold & Koekemoer 2841*, 2848 (4) PRE; 2869, 2875, 2893, 2897 (5) PRE; 2918 (4) PRE; 3181 (5) PRE; 3181a (4) PRE; 3248 (Ledbury, England), 3249 (Wageningen,

Netherlands), *CH13640* (1) PRE. *Pillans 4047*, 4048, 4233 (2) BOL. *Playford CH1324* (sub *M. wilmsii*) (4) PRE. *Pole-Evans 461* (5), *CH1351* (sub *M. wilmsii*) (4) PRE. *Porter CH3586* (5) PRE. *Potts 27*, *CH1312* (2) PRE. *Preiss 8282* (2) PRE. *Preuss 1192* (Cameroon) (5) BM.

Rankin 206 (3) BM. *C. Reid 816* (5) PRE. *Reichenbach 354137* (2) W. *Reinecke CH174* (5) PRE. *Rennie & Lambert 22* (sub *M. polymorpha*) (4) PRE. *Rogers TM 2269* (sub *M. polymorpha*) (4) PRE.

Scheepers 562 (sub *M. wilmsii*) (4) PRE. *Schelppe 2048* (5) BOL; 4226 (sub *M. wilmsii*) (2) BOL; 3745 (sub *M. wilmsii*) (4) BOL; 5359 (sub *M. parviloba*) (Zimbabwe) (4) BOL; 25367, 52542 (sub *M. wilmsii*) (2) BOL. *Scott CH3693* (5) PRE. *T.R. Sim CH1313*, *CH1316–CH1318*, *CH1322* (sub *M. tabularis*) (2) PRE; *CH1323* (sub *M. wilmsii*) (4) PRE; *CH1325–CH1327*, *CH1329*, *CH1330*, *CH1333* (5) PRE; *CH1339*, *CH1341* (sub *M. wilmsii*) (4) PRE; *CH1342*, *CH1344*, *CH1345* (5) PRE; *CH1347* (sub *M. wilmsii*) (4) PRE; *CH1352*, *CH1353* (5) PRE; *CH1356*, *CH1358* (sub *M. wilmsii*) (4) PRE. *SL CH1308* (2) PRE. *Smook 8746* (2) PRE. *Stokoe 9468* (sub *M. wilmsii*) (2) BOL. *Strauss CH13641* (4) PRE. *Symons CH1337* (5) PRE.

C. Tavares, P 66716 (3) LISU. *Theron 1339* (5) PRE. *Thorne CH1309*, *CH1544*, *CH3153* (2) PRE.

Univ. Durban-Westville 54 (5) PRE.

Van Breda 1116 (2) PRE. *Van der Bijl CH1332*, *CH1349*, *CH1354*, *NH16171*, *NH16175* (5) PRE. *Van Rooy 1012* (5), 1653 (4), 2624 (5) PRE. *A.E. Van Wyk 2066* (2) PRE. *Y. Van Wyk 883* (2) PRE. *Veltman 3*, 5 (4) PRE; 12 (5), 90 (4) PRE. *Venter 12200* (5) PRE. *Vorster 1785*, 1789 (5) PRE.

Wager CH3805 (sub *M. wilmsii*) (4) PRE. *Wagener CH13341* (2) PRE. *Wawra 10* (2) W.

Zenker 1339 (5) (typus) BM; 1898 (5) BR.