

## Studies in the Marchantiales (Hepaticae) from southern Africa. 6. The genus *Asterella* (Aytoniaceae: Reboulioideae) and its four local species

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**Keywords:** *Asterella*, *A. bachmannii*, *A. marginata*, *A. muscicola*, *A. wilmsii*, Aytoniaceae, Hepaticae, Marchantiales, *Phragmoblepharis*, Reboulioideae, section *Saccatae*, southern Africa

### ABSTRACT

A taxonomic account of the genus *Asterella*, and four local representatives, *A. muscicola*, *A. bachmannii*, *A. marginata* and *A. wilmsii*, subgenus *Phragmoblepharis*, is given here. A key to the species is provided. Two specimens identified by Arnell (1963) as *Reboulia hemisphaerica*, Collins 775 and Eyles CH 1175, are actually *A. wilmsii*; the presence of the genus *Reboulia* in southern Africa is therefore not confirmed and should be deleted from the annotated checklist by Magill & Schelpe (1979) and *Plants of southern Africa: names and distribution* (Arnold & De Wet 1993).

### UITTREKSEL

'n Taksonomiese verslag oor die genus *Asterella*, en vier van die plaaslike verteenwoordigers daarvan, *A. muscicola*, *A. bachmannii*, *A. marginata* en *A. wilmsii*, subgenus *Phragmoblepharis*, word hier gegee. 'n Sleutel tot die spesies word verskaf. Twee eksemplare, Collins 775 en Eyles CH 1175, wat deur Arnell (1963) as *Reboulia hemisphaerica* geïdentifiseer is, is in werklikheid *A. wilmsii*; die teenwoordigheid van die genus *Reboulia* in Suider-Afrika is dus nie bevestig nie en dit behoort geskrap te word van die geannoteerde kontrolelys deur Magill & Schelpe (1979) en van *Plants of southern Africa: names and distribution* (Arnold & De Wet 1993).

***Asterella*** P. Beauv. in Dictionnaire des sciences naturelles 3: 257 (1805); A. Evans: 247 (1920); Frye & L. Clark: 69 (1937); Hässel: 100 (1962); S.W. Arnell: 59 (1963); Vanden Berghen: 169 (1972); R.M. Schust.: 224 (1992). Type: *A. tenella* (L.) P. Beauv. (= *Marchantia tenella* L.), (lecto. designated by Long & Grolle 1992b).

*Fimbraria* Nees: 44 (1820); Gottsche *et al.*: 555 (1846); Schiffn.: 33 (1893); Steph.: 84 (1899); Sim: 22 (1926); K. Müll.: 353 (1952), nom. illeg. Lectotype: *F. marginata* Nees.

*Hypenantron* Corda: 648 (1829). Type: *H. ciliatum* Corda.

*Dictyochiton* Corda ex Nees: 258 (1838) nom. inval.

*Rhacotheca* Bisch.: 12 (1844). Type: *R. azorica* Bisch.

*Octokepos* Griff.: 343 (1849). Type: *O. khasyanum* Griff.

Thalloid, smallish to medium-sized to fairly large, flat-tish to slightly concave proximally, firm or rarely somewhat spongy, lime green to bright green, in crowded patches or dense mats; on soil at seepages and river banks or in drier, rocky locations. *Branches* simple, rarely once/twice pseudodichotomously furcate, or with latero-ventral or apical innovations; thickened over midrib, thinning toward margins, these from above somewhat scalloped, attenuate, frequently purple; apex slightly notched, with ventral scales recurring over edge.

*Dorsal epidermis* hyaline, unistratose, cells mostly thin-walled, lacking trigones, occasionally with a single large oil body; air pores small, simple, slightly raised, surrounded by 2 or 3 concentric rings of cells, 6–8 per ring, walls rarely radially thickened and pores then stellate; assimilation tissue with small, empty air chambers in several irregular layers or tall and in one layer, cells in bounding walls chlorophyllose but occasionally with an oil body; storage tissue with rounded or angular cells closely packed together; rhizoids both smooth and pegged. Scales mostly purple or wine-red, in 2 forwardly directed ventral rows, ovate to obliquely triangular, with one (rarely 2 or 3) lanceolate or acuminate appendage, scattered oil cells present, margins mostly entire.

Monoicous, paroicous or autoicous, rarely dioicous. *Androecia* sessile; antheridia in paroicous species in a cluster or a row immediately or somewhat further posterior to insertion of stalk; in autoicous or dioicous species, androecia well-defined, on reduced latero-ventral branches or as a median oval disc on main branch. *Archegoniophores* arising from apical notch, borne on stalk with or without air chambers and with one rhizoidal furrow, at the summit, with or rarely without paleae; head rounded or umbonate, nearly smooth to distinctly papillose, its air chambers opening via compound pores, below with (1–) 2–4(–5) lobes, each enclosing a capsule, the wall of the latter lacking thickening bands; involucre membranous, continuous with edges of lobes; pseudoperianth present, mostly pendulous, conical or blunt, vertically split into segments, but united at the tip, covering and projecting beyond the capsule in southern African species. *Spores* small to medium-sized to large, yellow, brown or fuscous, triangular-globular and winged, distal face rounded, mostly with regular or irregular network of large, angular to

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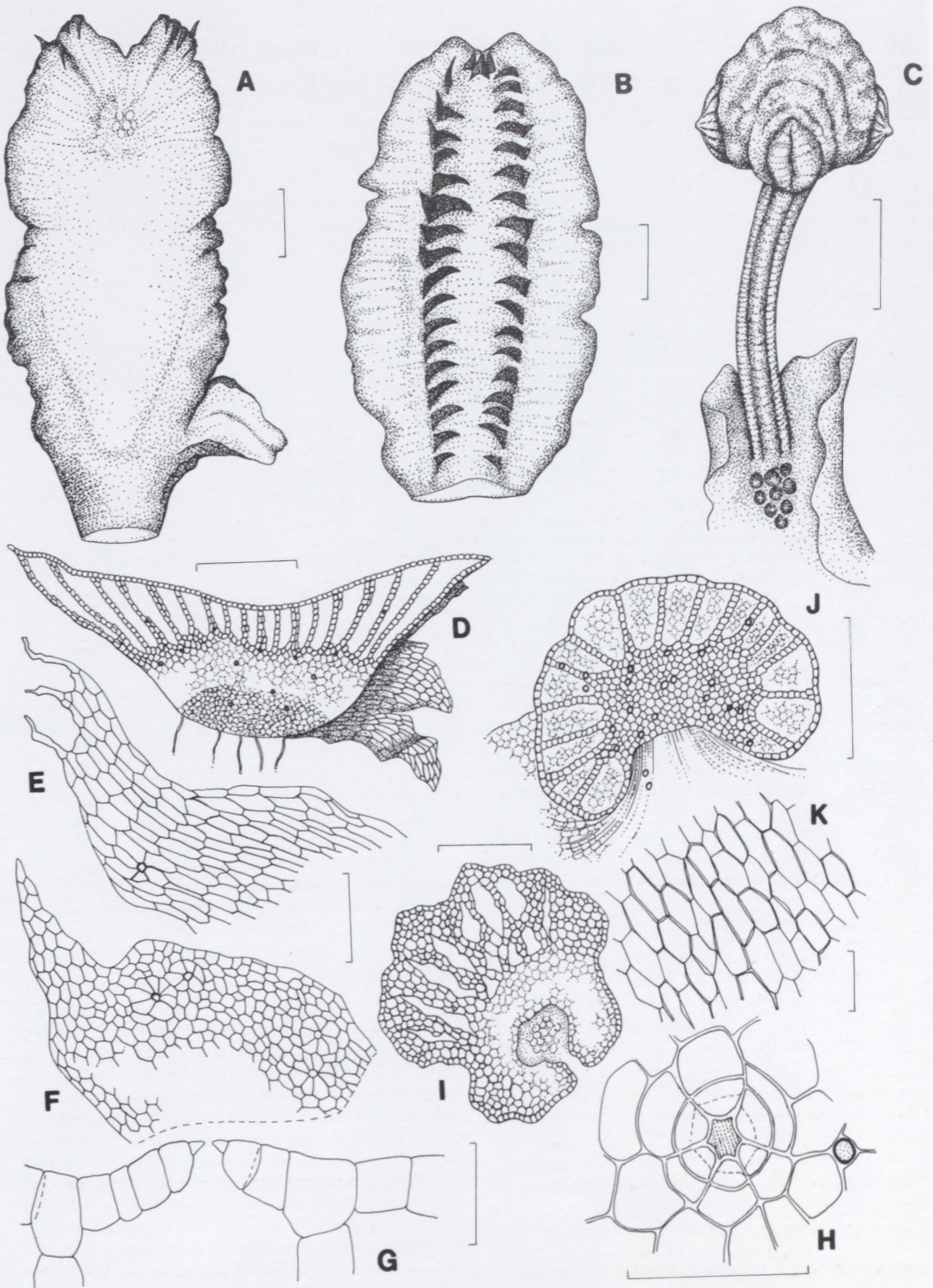


FIGURE 1.—*Asterella muscicola*. A, dorsal view of thallus; B, ventral view of thallus; C, carpocephalum raised on stalk and antheridia proximal to foot of stalk; D, transverse section of thallus; E, scale with fimbriate apex; F, scale with acuminate apex; G, transverse section of air pore; H, dorsal cells, air pore and oil cell from above; I, transverse section of stalk; J, longitudinal section of young archegoniophore; K, capsule wall cells. A–C, E, G, I, J, *Perold & Koekemoer 2968*; D, F, H, *Condy 13*; K, *Anderson 1248*. Scale bars: A–D, 2 mm; E, F, I, 250  $\mu$ m; J, 1 mm; G, H, K, 50  $\mu$ m.



rounded areolae, bordered by ridges and generally lined with small subsidiary areolae; proximal face with pronounced triradiate mark, its arms extending across undulating wing, each of three facets also with network of large and small areolae. *Elaters* short or of medium length, with 1–3 spirals. *Chromosome number*:  $n = 9$  or multiple thereof, or 10.

*Asterella* is one of the larger genera of the Marchantiales. It is classified in the family Aytoniaceae, subfamily Reboulinoideae. The genus *Asterella* has been divided into three subgenera: *Brachyblepharis*, *Asterella* and *Phragmoblepharis*, the latter with three sections, namely *Pappiae*, *Lindenbergianae* and *Saccatae* (Grolle 1976). *Asterella* species are easily recognized by the presence of a

basket-like pseudoperianth, which soon splits into narrow segments. It occurs world-wide and has had a long and controversial nomenclatural history, which is reviewed by Long & Grolle (1992a). Long & Grolle (1992b) have also submitted a proposal to conserve the generic name *Asterella* with a conserved type.

The four southern African species of *Asterella* are all placed in subgenus *Phragmoblepharis* Grolle (1976), since the segments of the pseudoperianths remain coherent at their tips for a long time, in contrast to those in subgenera *Brachyblepharis* and *Asterella*, where they separate at maturity. The last two subgenera are not found in southern Africa.

### Key to the southern African species of *Asterella*

- 1a Thalli spongy, with tall air chambers mostly in one storey, and then not subdivided by supplementary partitions, each opening dorsally by a stellate pore; ventral scales occasionally fimbriate at single lanceolate appendage; carpocephalum round or umbonate and lacking paleae at summit of stalk; pseudoperianth extending  $\pm 300 \mu\text{m}$  beyond involucre and subdivided into 12 or 13 segments; spores 75–95  $\mu\text{m}$  in diameter, dark brown, ornamentation with irregular zigzagging ridges . . . . . 1. *A. muscicola*
- 1b Thalli compact, firm, with small, low air chambers in several storeys, only some top ones opening above by a dorsal, non-stellate pore; ventral scales with 1 (or 2) lanceolate or ovate appendages, margin  $\pm$  entire; carpocephalum round or umbonate, papillose or  $\pm$  smooth, with paleae at summit of stalk; pseudoperianth extending more than 1000  $\mu\text{m}$  beyond involucre and subdivided into 14–16 segments; spores more than 100  $\mu\text{m}$  in diameter, yellow or brown, ornamentation with larger areolae generally containing subsidiary areolae:
- 2a Thalli smallest to large; carpocephalum covered with distinct papillae, projecting  $\pm 200 \mu\text{m}$ ; paleae at summit of stalk shaggy, dense, pale mauve or colourless, up to 3000  $\mu\text{m}$  long and 4 or 5 cells wide at base; ventral scales with lanceolate appendage; spores elaborately ornamented with 6–8 areolae across distal face, 20–30  $\mu\text{m}$  wide and ridges extending across wing, containing numerous subsidiary areolae (common, mostly summer rainfall species) . . . . . 2. *A. bachmannii*
- 2b Thalli medium-sized to very large; carpocephalum  $\pm$  smooth or with low papillae; paleae at summit of stalk colourless or purple, length variable; ventral scales with lanceolate or ovate appendages, spores less elaborately ornamented:
- 3a Thalli medium-sized; carpocephalum with umbonate head; paleae at summit of stalk mostly colourless, some very long, more than 8000  $\mu\text{m}$  in length,  $\pm 4$  cells wide at base; ventral scales with 1 or 2 lanceolate appendages; spores on distal face with (4–)6–9 areolae across,  $\pm 32 \mu\text{m}$  wide, very high ridges seldom extending across wing, usually containing small subsidiary areolae (winter rainfall species) . . . . . 3. *A. marginata*
- 3b Thalli large to very large; carpocephalum with rounded head, distinctly lobed below; paleae at summit of stalk almost colourless to purple, 2000–3000  $\mu\text{m}$  long, some up to 7 cells wide at base; ventral scales with single, large-celled, ovate appendage, constricted at base; spores on distal face with 5–8 areolae across, 25–30  $\mu\text{m}$  wide and extending to wing margin, almost empty of subsidiary areolae and hollow (summer rainfall, mostly Afrotropical species) . . . . . 4. *A. wilmsii*

1. *Asterella muscicola* (Steph.) S.W. Arnell: 60 (1963).

*Fimbraria muscicola* Steph.: 121 (1892); Steph.: 97 (1899), Sim: 22 (1926). Type: Transvaal, Spitzkop bei Lydenburg, Febr. 1888, leg. Dr Wilms G 001664, holo.! (G); G 024589, iso.! (G).

*Thallus* medium-sized to fairly large, grooved toward apex, slightly concave more proximally, dorsally bright green, margins soon turning purple along edge, becoming proximally wider (up to 1 mm) and pinkish purple (Figure 1A), polygonal outlines of subdorsal air chambers visible from above, i.e. reticulate dorsally, median areolae small, enlarging toward margins and then in parallel, radiating rows, air pores tiny, slightly raised, white 'specks', apparently solitary over each polygonal area, wet; thallus margins clasped together, revealing deep purple, transversely wrinkled underside of wings, dry; in crowded patches, simple or once/twice pseudodichotomously furcate. *Branches* 4–7(–13) mm long, total length up to 18 mm long, 2.5–3.5(–6.5) mm wide, in section 1250  $\mu\text{m}$  thick over midrib, laterally thinning out into attenuate wings, apex notched, with tips of 4–6 hyaline or purple-red ventral scales recurving over edge; margins acute, thin, scalloped, undulate, older parts dead, ventrally somewhat striate across, shiny, deep purple, flanks sloping obliquely;

ventral face medianly keeled, green, midrib with row of purple-red scales on either side (Figure 1B).

*Dorsal epidermis* unistratose, hyaline, purplish toward margins, cells thin-walled, without trigones at angles, from above 4- or 5(–7)-sided, (37.5–) 45.0–72.5  $\times$  15.0–25.0  $\mu\text{m}$ , in transverse section 25  $\mu\text{m}$  thick, rarely containing an oil body; marginal cells mostly 4-sided, variable in size, (17.5–)25.0–50.0  $\times$  15.0–40.0  $\mu\text{m}$ ; air pores very slightly raised, simple, small,  $\pm 7.5 \mu\text{m}$  wide, mostly 6-sided (Figure 1H), up to 137.5  $\mu\text{m}$  distant from each other, bounded by innermost circle of collapsed cellular remains, otherwise surrounded by 2 concentric rings of cells, each generally with 6 cells: inner cells bluntly triangular, smallest 12.5  $\times$  7.5  $\mu\text{m}$  at inner, narrower tip and 17.5  $\mu\text{m}$  at wider part, larger cells 22.5  $\times$  25.0  $\mu\text{m}$ , radial walls mostly thickened and pores thus stellate, outer row of cells (22.5–)25.0–32.5  $\times$  25.0–37.5  $\mu\text{m}$ , partly overlain by inner cells; assimilation tissue up to 650  $\mu\text{m}$  thick, with air chambers long and empty, in one layer (Figure 1D), or sometimes in several layers, particularly if section not exactly vertically cut and then seen in more than one plane, 90–150  $\mu\text{m}$  wide above, narrowing to  $\pm 50 \mu\text{m}$  wide below, vertical medianly, sloping obliquely toward margins, unistratose walls composed of cells, (30.0–)



37.5–47.5 × 32.5 µm in transverse section, when viewed from the front, 30.0–45.0 × 32.5–40.0 µm; occasionally with somewhat smaller cells containing an oil body, light brown to dark brown, smooth or finely warty, round, diameter ± 30 µm, almost entirely filling cell; storage tissue ± 600 µm thick, cells tightly packed together, angular, 20.0–37.5 µm wide, some with oil bodies, which are here more frequent than in air chamber walls; rhizoids smooth, ± 17.5 µm wide, or pegged and 22.5 µm wide. *Scales* wine-red to purple-red, arranged in 2 forwardly directed ventral rows, one on either side of midrib, not extending to margins of thallus, except at apex, obliquely triangular, 1100–1250 µm wide at curved base, above with acuminate appendage tapering to a narrow tip (Figure 1F), occasionally toward apex fimbriate (Figure 1E) and sometimes with several one- or two-celled marginal papillae, up to 37.5 × 10.0 µm, total length ± 1050 µm, including 170–350 µm long appendage, 8 or 9 cells wide where it joins body of scale, cells 5- or 6-sided, rarely rectangular, 57.5–100.0 × 25.0–32.5 µm, occasionally interspersed with scattered smaller, colourless cells (2–6 or 8), the oil body having been lost.

*Paroicus*. *Androecia* with antheridia in a group or in a short single or double row along midline of thallus and generally immediately proximal to stalk, i.e. basiscopic of archegoniophore (Figure 1C) or very rarely on separate plant, immersed, 350 × 250 µm, each opening above into a prominent, conical papilla, 220 × 100 µm. *Archegoniophores* single, rarely paired at apices of 2 furcating branches, almost sessile when young (Figure 1J), domed, air pores compound, leading below into air chambers, supported on and radiating outwards from central core of parenchymatous tissue, containing numerous oil cells, these also present in air chamber walls and epider-

mis. *Carpoccephala* at maturity raised on stalk (Figure 1C) arising at bifurcation of branches, the latter continuing in growth; stalk yellowish, shiny, erect or somewhat bent, 5–8 mm long, stout, 675 µm wide at ± midlength, becoming thicker toward base and tapering toward summit, in transverse section irregular in shape, with one rhizoidal furrow, 175 × 137 µm, cortical cells in single layer, thick-walled, brown, 12.5 × 12.5–15.0 µm, medullary cells thin-walled, 20.0–32.5 × 12.5–25.0 µm, with narrow to wide, open air chambers (Figure 1I); head rounded to somewhat umbonate, 3 mm across, bearing 4 or 5 capsules, the wall brown with unistratose cells lacking spiral thickenings, 4–6-sided, 50.0–57.5 × 20.0–25.0 µm; pseudoperianths extending obliquely downward and outward and projecting ± 300 µm beyond involucre, somewhat flattened sideways, in 12 or 13 cage-like, hyaline segments, each of which 550 × 150 µm, connate toward broad, blunt tips, at apex with small central nipple penetrated by a pore, cells in segments 4–6-sided, 47.5 × 22.5 µm, thick-walled. *Spores* 75–95 µm in diameter, triangular-globular, dark brown, opaque, wing somewhat pleated, 5 µm wide, margin undulate, distal face (Figure 2A–C) convex, reticulate, with very irregular, mostly incomplete areolae, the ridges forming an irregular, zig-zagging maze; proximal face (Figure 2D E) with distinct triradiate mark, facets also with irregular, incomplete areolae, ranging from small and crowded to larger and more widely dispersed. *Elaters* 150–175 µm long, 17.5 µm wide in centre, slightly tapering toward ends, doubly spiral (Figure 2F), light brown. *Chromosome number*: n = 10 (T. Bornefeld pers. comm.)

#### DISCUSSION

This species of *Asterella* has tall air chambers and was initially placed in the group Spongiosae, together with *A.*

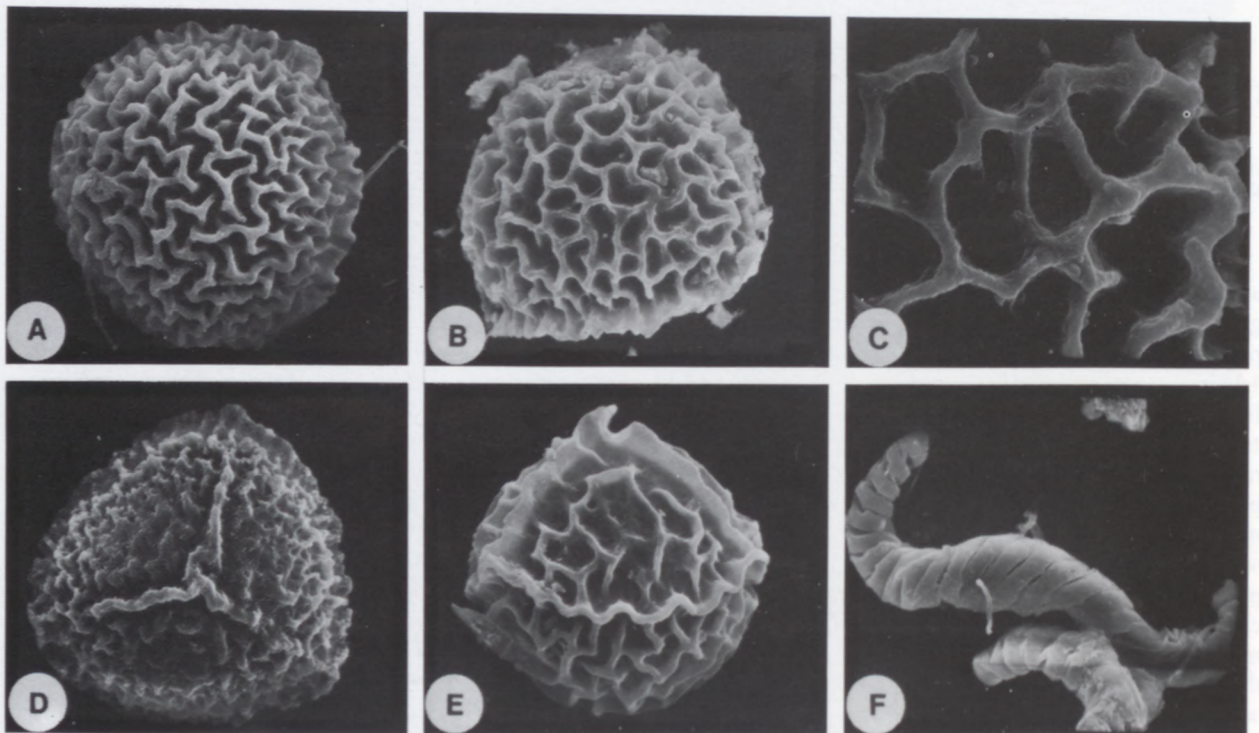


FIGURE 2.—SEM micrographs of *Asterella muscicola*. A–E, spore: A, distal face; B, distal side view; C, areolae on distal face much enlarged; D, proximal face; E, side view. F, elater. A, D–F, *Perold & Koekemoer* 2968; B, C, *Marais* 832. A, D, E, × 490; B, × 320; C, × 952; F, × 460.



*pilosa* and *A. tenera*, by Stephani (1892). It was illustrated by him in his *Icones* (Microform 1985 seen by me). Later on, Stephani (1899) proposed a new classification based on the shape of the female receptacle and he then placed it in group B, Capituli centrum hemisphaericum. Nowadays it is classified in subgenus *Phragmoblepharis* Grolle, (since the pseudoperianth segments remain attached at their tips when mature), and in its section *Saccatae*, (since the summit of the stalks lack paleae).

Sterile specimens of *A. muscicola* have been confused with *Athalamia spathysii*, since the dorsal air pores are also stellate. The air chambers are likewise devoid of chlorophyllose filaments, but oil bodies are more numerous and their remains are present in the scales which have cells half as wide as those in *A. spathysii*. It differs from *Athalamia* species mainly in sporophyte characters: the stalk arises at the bifurcation of the branches, it is thicker and has a rhizoidal furrow, its cortical cells differ from those in the medulla where air chambers are present, it is devoid of scales both at the base and summit (Arnell (1963) erroneously refers to scales at the top), the cells in the capsule wall lack annular or semi-annular thickenings, pseudoperianths are present, the spores are larger, dark brown and winged, their ornamentation is reticulate (not papillose), the shape is triangular-globular with a distinct triradiate mark on the proximal face and the elaters are shorter and wider. Mycorrhiza are present in the storage tissue, having entered via the rhizoids. Vegetative reproduction is rarely by ventral stolons.

Quite a number of *Asterella* specimens held at PRE had been incorrectly identified as *A. muscicola*, even by Arnell (1957), who also misnamed a Volk collection of *Athalamia spathysii* from Namibia as *Asterella muscicola* (Volk 1979). Sim (1931) also reported *A. muscicola* from South West Africa [Namibia] but this has not been confirmed; in fact, according to Volk (1979), Grolle had informed him (pers. comm.) that *A. muscicola* does not grow in Namibia.

The type specimens consist of only a few fragments and were collected east of Lydenburg, south of the present town of Sabie, Eastern Transvaal. The species is probably endemic to southern Africa and is known from Botswana, the North-West (northeastern Cape & southeastern Transvaal), Northern and Eastern Transvaal (type specimen), KwaZulu/Natal, Orange Free State, Lesotho, and Eastern Cape (Figure 3). Its range extends into Malawi (Kasunga Nat. Park, *Perold* 2682) and Zimbabwe (*Eyles* 932, 933; *Miller* 7869) from where it is also reported by Best (1990). It frequently grows at high altitudes on soil overlying sandstone or basalt outcrops in association with other liverworts such as *Plagiochasma* spp. and *Riccia* spp.

2. *Asterella bachmannii* (Steph.) S.W. Arnell, *Hepaticae of South Africa*: 62 (1963). Type: Pondoland, Port Grosvenor, *Bachmann* (13866 G, lecto.!, 13867 G!).

*Fimbraria bachmannii* Steph.: 7 (1894); Steph.: 105 (1899), Sim: 22 (1926).

*Thallus* smallish to medium-sized to quite large, firm and compact, dorsally flat, light green, rather crystalline to shiny when fresh, margins turning purple on exposure to sun (Figure 4A), crinkled outlines of small subdorsal air chambers faintly or not visible from above, air pores

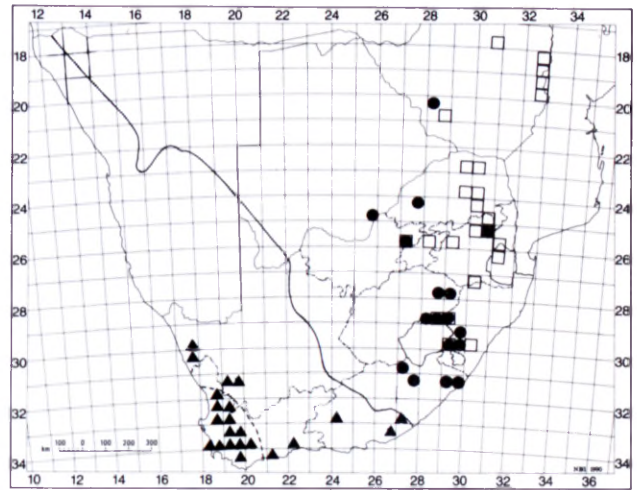


FIGURE 3.—Distribution of *Asterella muscicola*, ●, *A. wilmsii*, □, in southern Africa and Zimbabwe; and *A. marginata*, ▲, in southern Africa. Summer rainfall area: to the right of the solid line. Summer and winter rainfall area: to the left of the solid line. Winter rainfall area: to the left of the broken line.

tiny, slightly raised and scattered, wet; thallus margins raised or inflexed, sometimes inrolled and tightly clasped together, dry; in crowded, overlying mats, simple or occasionally once, rarely several times pseudodichotomously furcate, often with apical or latero-ventral innovations. Branches broadly ligulate, widening rapidly from narrow base, when simple up to 17 or 18 mm long, when branched total length up to 25 mm, with terminal branches 3–4 mm long and moderately divergent, (1.9–)2.5–4.0 (–4.9) mm wide, (450–)500–600(–775)  $\mu\text{m}$  thick over midrib, laterally thinning out into attenuate wings, apex slightly notched, with tips of a few ventral scales recurving over edge; margins acute, thin, slightly scalloped, somewhat undulate; ventrally green or red to deep purple, laterally somewhat striate across obliquely sloping flanks, medianly keeled, midrib with row of purple scales on either side (Figure 4B).

*Dorsal epidermis* unistratose, generally containing chloroplasts, from above cells (4–)5- or 6-sided, thin-walled, (30.0–)50.0–67.5(–90.0)  $\times$  22.5–30.0  $\mu\text{m}$ , their orientation changing from apically directed medianly to outwardly sloping laterally in transverse section, (20–)25–35  $\mu\text{m}$  thick, occasionally containing a round oil body, 25  $\mu\text{m}$  across, almost filling cell; marginal cells in 1 or 2 rows, long- or short-rectangular (Figure 4G), occasionally 5-sided, 30.0–50.0  $\times$  (12.5–)17.5–22.5  $\mu\text{m}$ ; air pores slightly raised (Figure 4F), simple, small, oval, up to 17.5  $\times$  12.5  $\mu\text{m}$ , 110–150  $\mu\text{m}$  distant from each other (Figure 4E), bounded by innermost circle of collapsed cells, and outwardly surrounded by 2 intact, partly overlying concentric rings of 6–8(–10) cells in each, inner ones smaller,  $\pm$  12.5  $\times$  15.0–20.0  $\mu\text{m}$ , outer ones bluntly wedge-shaped, up to 15–20  $\times$  25–35  $\mu\text{m}$ , radial walls not thickened; assimilation tissue up to 280  $\mu\text{m}$  thick, with small, empty air chambers (Figure 4D), 37.5–75.0  $\mu\text{m}$  wide, in 2–4 storeys, toward margins elongating and sloping obliquely, chlorophyllose cells in bounding walls rounded or oval, 25.0–30.0  $\times$  22.5–32.5  $\mu\text{m}$ ; storage tissue mostly confined to keel,  $\pm$  360  $\mu\text{m}$  thick, cells angular, isodiametric, (17.5–)25.0–35.0  $\mu\text{m}$  wide, closely packed together, walls thick and pitted, an occasional cell



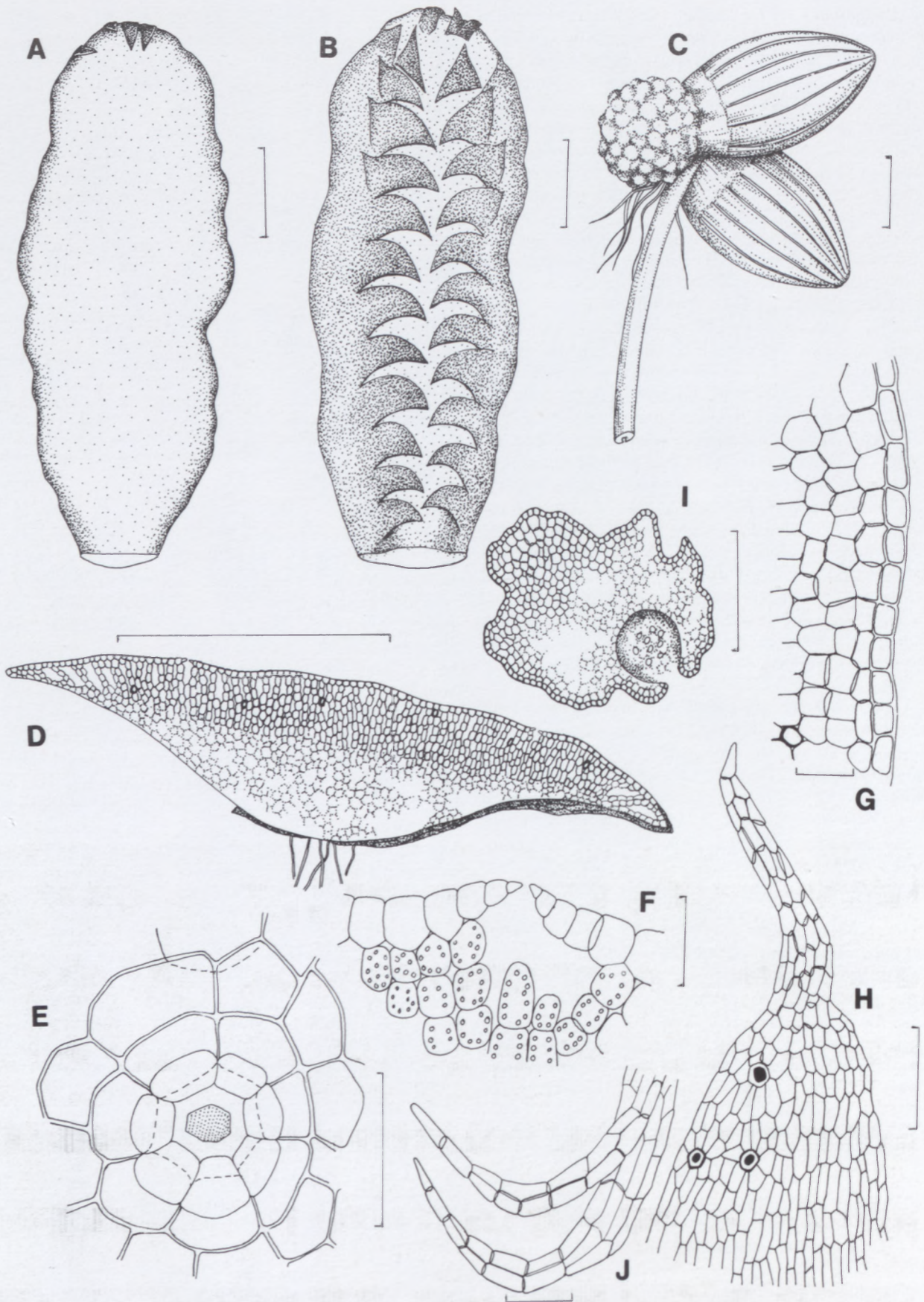


FIGURE 4.—*Asterella bachmannii*. A, dorsal view of thallus; B, ventral view of thallus, appendages of scales mostly not visible against dark purple flanks; C, carpocephalum with papillose disc and two pseudoperianths; D, transverse section of thallus; E, air pore and surrounding cells from above; F, transverse section of air pore; G, marginal cells; H, appendage and upper part of scale; I, transverse section of stalk; J, paleae. A–D, I, *Glen 2150*; E, G, H, J, *Perold & Koekemoer 2856*; F, *Condy 7*. Scale bars: A–D, 1 mm; E–G, 50 μm; H, I, 250 μm; J, 100 μm.



with oil body; rhizoids arising from ventral surface numerous, smooth, 15–20(–30)  $\mu\text{m}$  wide, or pegged, 7.5–17.5  $\mu\text{m}$  wide. Scales (Figure 4H) red to deep purple, arranged in 2 forwardly directed ventral rows, one on either side of midrib, not extending to margins of thallus, obliquely triangular, usually with a single lanceolate appendage, occasionally with two, 450–650(–800)  $\mu\text{m}$  long, constricted at base, 150–200  $\mu\text{m}$  wide, tapering above to a conical apical cell, 50.0–87.5  $\times$  7.5–17.5  $\mu\text{m}$ , lower cells 95.0–125.0  $\times$  32.5–37.5  $\mu\text{m}$ , body of scale up to 1000  $\mu\text{m}$  long and 1500  $\mu\text{m}$  wide at its crescentic base, cells 4–6-sided, 50.0–77.5  $\times$  25.0–35.0  $\mu\text{m}$ , scale tapering to narrow 'tail' below, cells long and narrow, 82.5–122.5  $\times$  12.5  $\mu\text{m}$ ,  $\pm$  8 smaller, colourless cells per scale, 35  $\times$  35  $\mu\text{m}$ , containing remains of oil body.

?Dioicous, rarely autoicous. *Androecia* extending backwards in median patch from apex of main branch, rarely with a second one at a midlength constriction, or, sometimes on short apical or lateral innovations, antheridia immersed in sessile, elongated or oval cushions,  $\pm$  3000  $\times$  750  $\mu\text{m}$ , lacking scales and opening above via stout, raised, purple-red papillae, 150  $\mu\text{m}$  long. *Archegoniophores* proximal to apical notch of main branch or rarely on short latero-ventral innovations, single, occasionally paired at apices of 2 forking branches, almost sessile when young, with numerous ( $\pm$  75), long, pale, sometimes purple, paleae arching over disc. *Carpocephala* at maturity raised on stalk, arising 1.5 mm back from apex of branch in apical notch, its foot sometimes in a shallow, rounded depression proximally, its length variable, (1–)5–13(–20) mm long, whitish to purple, widening toward base, in transverse section at  $\pm$  midlength (Figure 1I) 550  $\times$  450  $\mu\text{m}$ , with single rhizoidal furrow, cortical cells in a single layer, slightly thicker-walled, 17.5  $\times$  12.5  $\mu\text{m}$ ,

medullary cells angular,  $\pm$  25.0  $\times$  17.5  $\mu\text{m}$ ; at summit of stalk  $\pm$  32 slender, shaggy paleae, white or purple, up to 3250  $\mu\text{m}$  long, 4 or 5 cells wide at base, cells 120–137  $\times$  25  $\mu\text{m}$ , gradually tapering to conical apical cell, 67.5  $\times$  20.0  $\mu\text{m}$  (Figure 4J); disc rounded,  $\pm$  3 mm across when bearing 4 or 5 capsules, but frequently with only 1 or 2 capsules (Figure 4C) and then smaller, above with numerous prominent papillae, outwardly projecting  $\pm$  200  $\mu\text{m}$  and enclosing air chambers which open above via compound air pores; membranous involucre partly covering capsules below, the latter spherical, 1000  $\mu\text{m}$  across, the wall turning brown, unistratose, cells lacking spiral thickenings, 4–6-sided, 62.5–80.0  $\times$  27.5–37.5  $\mu\text{m}$ , toward apex of capsule cells shrinking and their walls thickening, with trigones at corners, the wall dehiscing along well-defined line and inner basal part remaining attached; pseudoperianths descending obliquely downward and extending  $\pm$  1000  $\mu\text{m}$  beyond involucre, generally split into 14 cage-like segments, shiny white or purple-stained, up to 2375  $\mu\text{m}$  long and 750  $\mu\text{m}$  wide at widest part, tapering to narrow tips where coherent with other segments, the cells elongated, 175–258  $\times$  37  $\mu\text{m}$ , becoming shorter toward tip. Spores 102.5–125.0  $\mu\text{m}$  in diameter, triangular-globular, mostly yellow, sometimes brown, translucent, wing undulate, up to  $\pm$  20  $\mu\text{m}$  wide, margin crenulate, distal face (Figure 5A, B) convex, with network of 6–8 angular areolae across, 20–30  $\mu\text{m}$  wide, ridges 7.5–10.0  $\mu\text{m}$  high and laterally extending across wing, hollow floor of areolae highly porate (Figure 5C) and generally with smaller subsidiary areolae (Figure 5A), sometimes with ornamentation becoming very elaborate (Figure 5B) and always extending over crests of main ridges and across wing to margin; proximal face with prominent triradiate ridge (Figure 5D, E), its arms  $\pm$  15  $\mu\text{m}$  high and continuous from the pole across wing to margin, each of

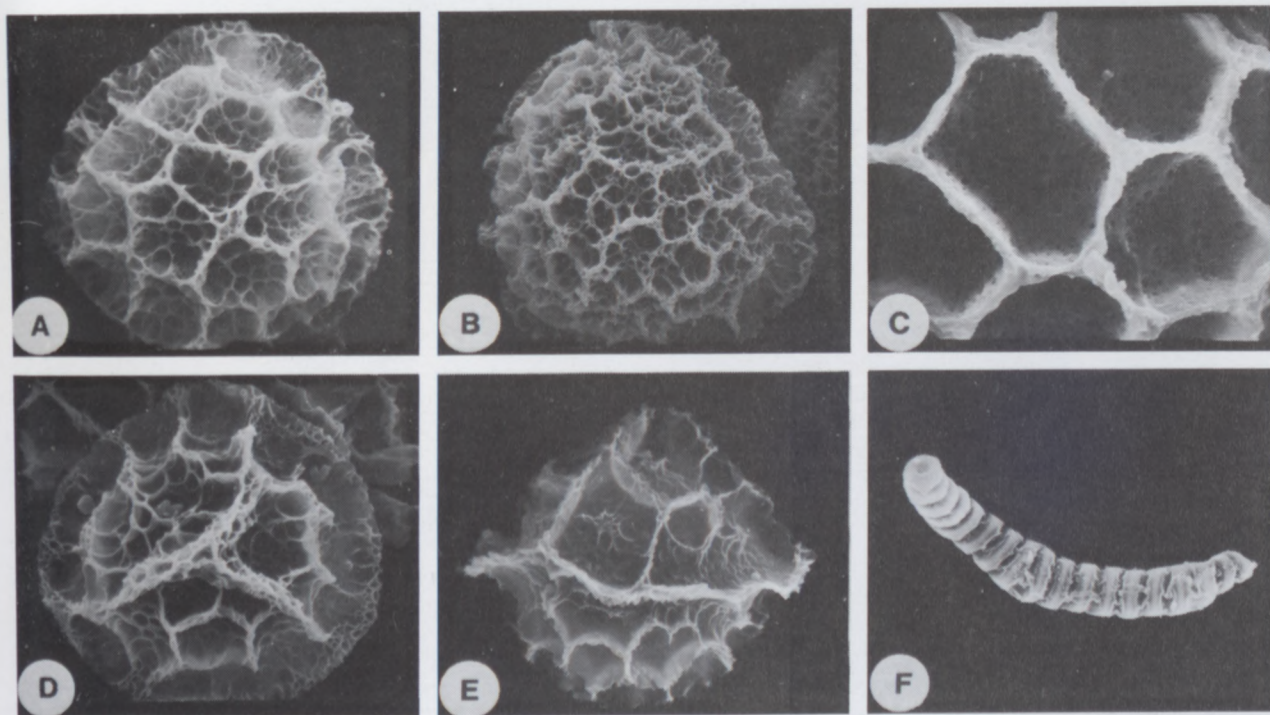


FIGURE 5.—SEM micrographs of *Asterella bachmannii*. A–E, spore: A, distal face with primary and subsidiary areolae; B, distal face, seen slightly from side, with more highly ornamented areolae; C, much enlarged areolae on distal face, lacking subsidiary areolae, but highly porate; D, proximal face; E, side view. F, elater. A, *Glen* 2155; B, *Dieterlen* 1142; C, *S.M. Perold* 2703; D, *Perold & Koekemoer* 2917; E, *Perold & Koekemoer* 2874; F, *Perold & Koekemoer* 2856. A, D, E,  $\times$  400; B,  $\times$  430; C,  $\times$  1000; F,  $\times$  416.



3 facets with areolae,  $\pm 10 \mu\text{m}$  wide, also extending across wing and containing numerous (Figure 5D) or fewer (Figure 5E), smaller, subsidiary areolae that cross over crests of main areolae and onto wing to margin, which is finely ornamented on both faces. *Elaters* 142–165(–180)  $\mu\text{m}$  long, and 15  $\mu\text{m}$  wide in centre, slightly tapering to the ends, doubly spiral (Figure 5F), yellow. *Chromosome number*:  $n = 9$ . (T. Bornefeld pers. comm.)

#### DISCUSSION

*Asterella bachmannii* is a variable species and can range in size from smallish to quite large. The thallus margins and ventral face can be very deeply pigmented or hardly at all, depending on whether it is exposed to intense sunlight or not. The ventral scales can likewise be deeply pigmented and the appendages are then not clearly discernible against the purple flanks as in Figure 4B. It can be distinguished from *A. muscicola* by the compactness of the assimilation tissue and from *A. wilmsii*, by its smaller size and the lanceolate appendages (occasionally double) of the purple or reddish purple ventral scales and from *A. marginata* by its generally purple, not wide, black thallus margins and by its mostly summer rainfall distribution. Sterile specimens with lanceolate scale appendages that had been collected in the summer rainfall areas (Figure 3: area to the right of the solid line) have not been named, although there can be little doubt that they should also be placed under *A. bachmannii*. *Asterella bachmannii* and *A. marginata* are, however, sympatric in the Western and Eastern Cape, where the winter and summer rainfall seasons overlap (Figure 3: area to the left of the solid line), and here too only specimens with carpocephala have been named. Fertile plants of *A. bachmannii* are easily recognized by the mostly pronounced papillae on the disc of the carpocephalum as well as by the dense, narrow, stringy or shaggy paleae which are usually white, but occasionally can be purple-stained. The spores are highly ornamented with the main areolae containing numerous smaller subsidiary areolae on both faces, giving it a lacey appearance. Spores from all available sporulating material were photographed by SEM and the spore ornamentation proved to be the most consistently uniform character, except in immature spores and in some old spores which had become shrivelled.

The sexuality is difficult to determine, as the plants form dense overlying mats with apical and latero-ventral innovations; rarely could it be conclusively ascertained that an androecium grew on a short lateral innovation of a main branch with a carpocephalum at the apex and even more rarely, both a carpocephalum and an androecium were found on lateral innovations of the same main branch.

*Asterella bachmannii* is common and by far the most frequently collected *Asterella* species in the summer rainfall areas of southern Africa. It is known from Botswana, the North-West, Northern and Eastern Transvaal, the PWV (central Transvaal), Swaziland, KwaZulu/Natal, Orange Free State, Lesotho, Eastern and Western Cape (Figure 6). It is mostly found on damp soil along stream banks, at waterfalls or in shaded gulleys or kloofs, sometimes on soil-covered vertical rock walls at seepages or on soil overlying sandstone, in light shade or in full sunlight. It

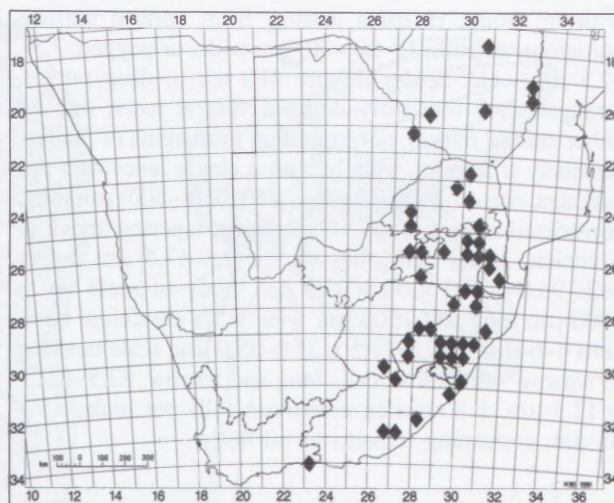


FIGURE 6.—Distribution of *Asterella bachmannii* in southern Africa (and Zimbabwe).

occasionally grows together with *A. wilmsii*, *Symphyogyna* species and *Fossombronina* species. Its range extends into Zimbabwe (Eyles CH 776, CH 1122, CH 1276; Miller CH 4250; Schelpe 4009, 5359; Sim CH 1213, CH 1249) and Malawi (Perold 2573, Nyika Nat. Park). Best (1990) has also reported it from Zimbabwe. It is thought that the specimens from Zaïre (Schmidt 258, 7188) identified and described by Vanden Berghen (1972) as *A. marginata* should be placed here, since the carpocephalum disc is markedly papillose and the ventral scale, as illustrated by him, has two acuminate appendages, which I also sometimes found in *A. bachmannii*. In *A. marginata* most of the paleae are generally much longer and its distribution is moreover apparently confined to the winter rainfall area (Figure 3: area to the left of the broken line) of the Western Cape with outliers in the Eastern Cape.

3. *Asterella marginata* (Nees) S.W. Arnell, *Hepaticae of South Africa*: 63 (1963). Type: Capite b. spei, crescit iuxta viam in monte Leuwenstaart ad terram, leg. Bergius (BM).

*Fimbraria marginata* Nees: 44 (1820); Gottsche *et al.*: 559 (1846); Steph.: 104 (1899).

*Thallus* medium-sized, firm and compact, dorsally flat-fish to somewhat concave, bright green, marginally with narrow to mostly wide black or occasionally reddish purple border (Figure 7A), shiny to dull, outlines of sub-dorsal air chambers hardly visible from above, air pores slightly raised and scattered, wet; thallus margins raised to inrolled, dry; in crowded mats, simple or once, rarely twice pseudodichotomously furcate, sometimes with apical or latero-ventral innovations. *Branches* obovate to obcordate, or ligulate, frequently widening rapidly from narrow base, up to 23 mm long, with terminal branches 10–15 mm long and moderately to widely divergent, 2.3–5.0 mm wide, 550–565  $\mu\text{m}$  thick over midrib, laterally thinning out into attenuate wings, apex notched, with appendages of apical scales recurving over edge; margins acute, thin, very wavy to almost frilly; ventrally green over midrib, but partly covered by row of purple scales on either side (Figure 7B), flanks purple to black and obliquely sloping (Figure 7D).



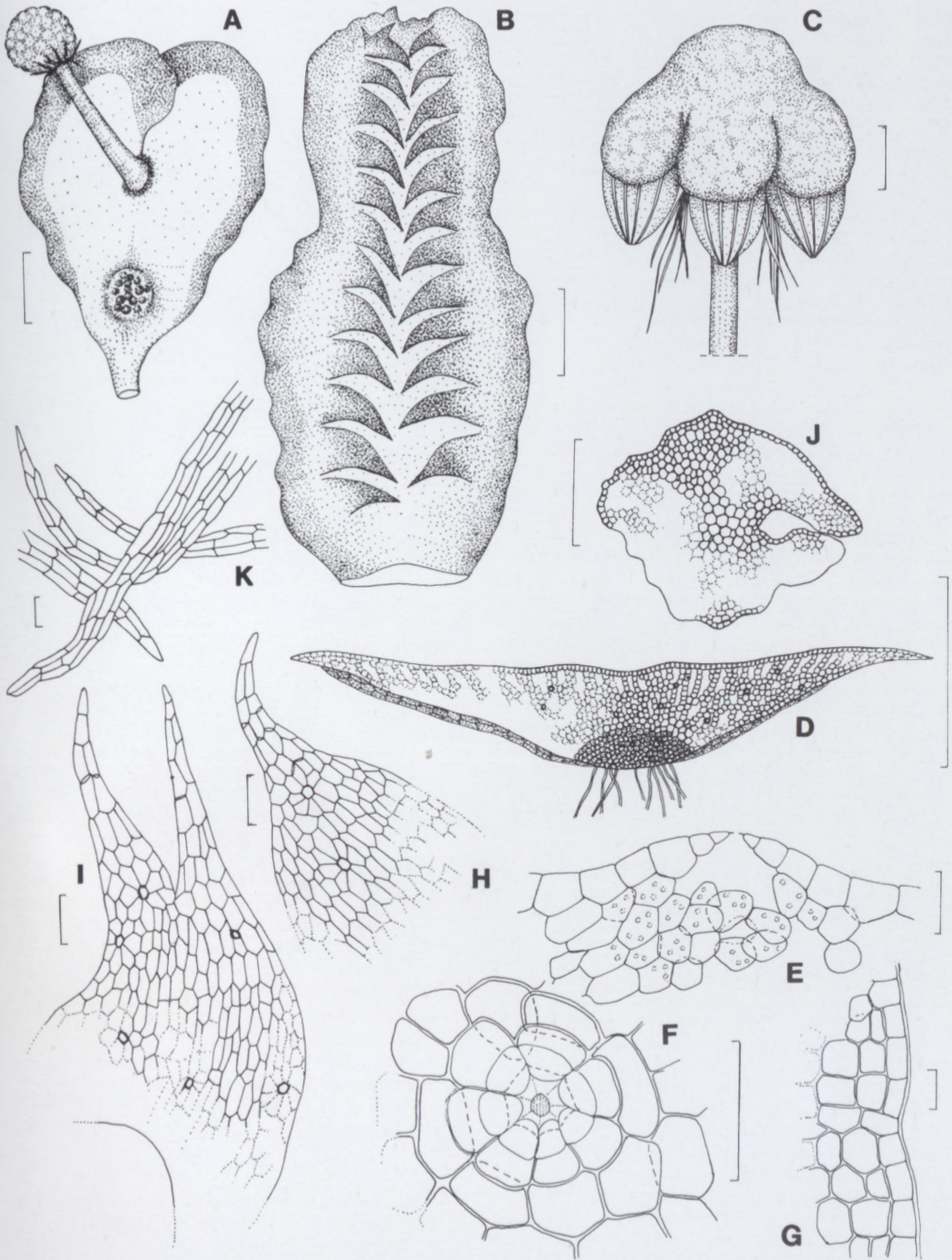


FIGURE 7.—*Asterella marginata*. A, dorsal view of thallus with young carpocephalum raised on stalk and sessile androecium; B, ventral view of thallus; C, carpocephalum with pseudoperianths; D, transverse section of thallus; E, transverse section of air pore; F, air pore and surrounding cells from above; G, marginal cells; H, ventral scale with one appendage; I, ventral scale with 2 appendages; J, transverse section of stalk; K, paleae. A, B, D–F, H, I, *S.M. Perold* 2787; C, *Pillans* 3991; G, *Arnell* 505; J, *Arnell* 206; K, *Koekemoer* 316. Scale bars: A–D, 1 mm; E–G, 50  $\mu$ m; H–J, 250  $\mu$ m; K, 100  $\mu$ m.



*Dorsal epidermis* unistratose, from above cells 5- or 6-sided, walls thin but slightly thickened at corners, 30.0–45.0 × 17.5–20.0 µm, in transverse section 27.5–37.5 µm thick; marginal cells in 1 or 2 rows (Figure 7G), short-rectangular, 25 × 30 µm, or isodiametric, 27.5 × 27.5 µm, or irregular in shape; air pores slightly raised (Figure 7E), simple, oval, small, ± 10.0 × 7.5 µm and up to 117.5 µm distant from each other, bounded by innermost ring of collapsed cells, ± 5 µm wide, outwardly surrounded by 2 intact, partly overlying concentric rings of 5–7 cells in each, inner ones smaller (Figure 7F), 10.0–12.5 × 12.5–22.5 µm, outer ones 15.0–17.5 × (17.5–) 25.0–35.0 µm; assimilation tissue 200–250 µm thick, with small, empty air chambers in top 2 or 3 storeys, 12.5–42.5 µm wide, becoming larger in lowest storey, up to 75 × 50 µm, chlorophyllose cells in bounding walls rounded to oval, 20.0–35.0 × 22.5–27.5 µm, quite frequently with round oil body, ± 20 µm in diameter and almost filling cell; storage tissue confined to keel, ± 300 µm thick, cells angular and closely packed together, 22.5–45.0 µm wide, some containing an oil body, cell walls porate, thickened, often with striate network of thickening bands; rhizoids numerous, some pegged, 10–15 µm wide, others smooth, 15–22 µm wide. *Scales* (Figure 7H, I) deep purple to lightly pigmented, in two forwardly directed ventral rows, one on either side of midrib, not extending to thallus margins, triangular to obliquely triangular, with 1 or 2(3) lanceolate, apically shortly acuminate appendages, equal in length or not, 675–925 µm long, tapering to single apical cell, ± 105 × 15 µm, lower cells ± 100.0 × 27.5 µm, gradually becoming shorter, ± 40.0 × 22.5 µm, toward unstricted base, ± 375 µm wide, body of scale ± 675 µm long, 825–925 µm wide at crescentic base, cells 55–125 × 27–32 µm, 5- or 6-sided, walls somewhat sinuate, tapering below to narrow 'tail', where cells long-rectangular, 70–150 × 10–12 µm, oil body remains in up to ± 20 cells per scale, colourless, rounded, 37.5 × 30.0 µm, a few small mucilage papillae at lateral scale margin.

Autoicous or monoicous. *Androecia* in sessile cushions on latero-ventral innovations or at base of main branches (Figure 7A), antheridia immersed and opening above via raised, purple papillae. *Archegoniophores* proximal to apical notch of main branch, single, occasionally paired at apices of two furcating branches, almost sessile when young. *Carpocephala* at maturity raised on stalk, arising ± 1 mm back from apex of branch in apical notch, its foot slightly wider than midlength dimensions of ± 575 × 600 µm, in transverse section (Figure 7J) with a single rhizoidal furrow, 85 µm wide, cortical cells in one layer, slightly thicker-walled on outside, small and rounded, ± 17.5 × 17.5 µm, medullary cells angular, 15–30 µm wide, length of stalk variable, 2.5–18.0 mm, white or reddish purple, at its summit (and along its length) with numerous pale, occasionally purple paleae (Figure 7K), some of them very long, up to 8400 µm, others 1250–2750 µm, base ± 100 µm or 4 cells wide, tapering to single apical cell, 95 × 30 µm, lower cells 125 × 27 µm; disc ± 3 mm across, umbonate (Figure 7C), air pores compound, slightly raised and sometimes quite conspicuous, (1–)3–5(–6) capsules borne below, each encased in pseudoperianth which descends obliquely downward, extending ± 1100 µm beyond the involucre and divided into 15 segments, these 2125 µm long and 550 µm wide at widest part, tapering toward coherent tip, cells (4–)5- or 6-sided, 90.0–

137.5 × 25.0–37.5 µm, lower down smaller, ± 50 × 25 µm. *Spores* (102–)125–140 µm in diameter, triangular-globular, yellow, translucent, wing undulate, up to 20 µm wide, margin crenulate, distal face (Figure 8A, B) convex, centrally with (4–)6–9 complete areolae, ± 32.5 µm wide, outer areolae incomplete, the ridges up to 12.5 µm high, seldom extending across wing, smaller, subsidiary areolae, 2.5–5.0 µm wide (and occasionally even further divided up), generally covering floor of larger areolae and extending over crests of main ridges (Figure 8C); proximal face with prominent triradiate mark (Figure 8D, E), its arms 15 µm high and continuous from the pole across wing to margin, each of 3 facets with complete or mostly incomplete areolae, main ridges sometimes extending across wing, small subsidiary areolae covering floor and ridges of main areolae, as well as arms of triradiate mark. *Elaters* ± 145 µm long, 12.5 µm wide in centre, slightly tapering to the ends, doubly spiral (Figure 8F), yellow. *Chromosome number*: n = not known.

## DISCUSSION

*Asterella marginata* has frequently been confused with *A. bachmannii*, in fact, Arnell (1963) stated that he could find no real differences between them, basing his opinion on their scale appendages, air pores, epidermal cells and spores. The result is that many specimens held at PRE and BOL, have been wrongly identified. Sterile collections of *A. marginata* are indeed difficult to place. In fertile specimens, however, the umbonate head of the carpocephalum, which lacks prominent papillae and the frequently very long, pale paleae, as well as the spore ornamentation mostly with numerous fine, ± regular, subsidiary areolae contained within the highly ridged, larger ones, which usually do not extend across the wing, make it quite easily recognizable. Its distribution, moreover, appears to be confined to the winter rainfall areas of the Western and Eastern Cape, the latter being the only area where *A. marginata* (Figure 3) and *A. bachmannii* (Figure 6) occur together. Previous reports of *A. marginata* from elsewhere (Stephani 1899; Arnell 1963; Vanden Berghen 1972; Best 1990) should be treated with reservation. As noted under *A. bachmannii*, Vanden Berghen's (1972: fig. 75A) illustration of *A. marginata*, with prominent papillae on the carpocephalum head, suggest it to be the former species, and not the latter.

*Asterella marginata* grows in dense mats on clayey soil or on weathered, soil-covered rocks at seepages or riverbanks, between rock crevices and under ledges, sometimes in association with *Fossombronina* spp., *Bryum* spp. and *Riccia* spp.

4. *Asterella wilmsii* (Steph.) S.W. Arnell, Hepaticae of South Africa: 62 (1963). Type: Spitzkopf bei Lydenburg, Transvaal, leg. Dr Wilms (ex Herb. Jack, (001666 G, lecto. fide in litt. Grolle!) selected here; ex Herb. Steph. 024590 G!).

*Fimbraria wilmsii* Steph.: 122 (1892); *ibid.*: 103 (1899); Sim: 23 (1926).

*F. angolensis* Steph.: 100 (1899); *Asterella angolensis* S.W. Arnell: 64 (1963). Type: Angola, Huilla, waterfall, *Newton 25a* (001673 G, holo.) fide Grolle (on specimen packet).



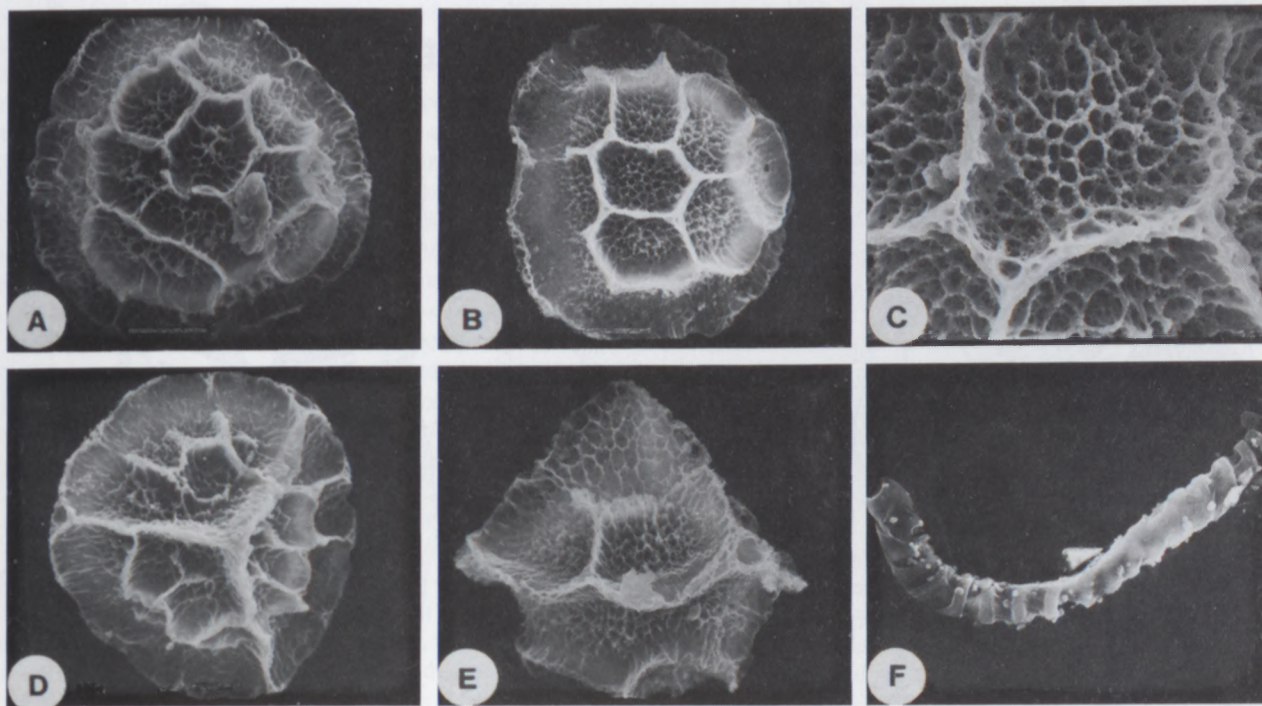


FIGURE 8.—SEM micrographs of *Asterella marginata*. A–E, spore: A, distal face; B, distal face seen slightly from the side; C, much enlarged areolae with inner subsidiary areolae; D, proximal face; E, side view. F, elater. A, Arnell 267; B, C, E, S.M. Perold 2418; D, Arnell 505; F, S.M. Perold 2092. A,  $\times 340$ ; B,  $\times 424$ ; C,  $\times 990$ ; D,  $\times 304$ ; E,  $\times 408$ ; F,  $\times 493$ .

*Thallus* large, thin but compact, dorsally flat to slightly concave, yellowish green, margins gently scalloped, dark red (Figure 9A), pigmentation becoming diffuse inwardly, outlines of subdorsal air chambers not visible from above, air pores hardly raised, wet; thallus margins slightly raised to inflexed or sometimes inrolled, dry; in crowded, overlying mats, mostly simple or once pseudo-dichotomously furcate, sometimes with apical or latero-ventral innovations. *Branches* broadly ligulate, widening rapidly from narrow base, 30–40(–75) mm long, if furcate, terminal branches up to 10 mm long, narrowly to moderately divergent, 4.7–7.1 mm wide; 600–800(–950)  $\mu\text{m}$  thick over midrib, laterally thinning out into attenuate wings (Figure 9D), apex notched with appendages of hyaline to deep purple ventral scales recurving over edge; margins acute, thin, somewhat undulate; ventrally reddish purple, laterally striate across, flanks sloping obliquely, medianly keeled, green, midrib with row of purple-red scales on either side (Figure 9B).

*Dorsal epidermis* unistratose, cells containing chloroplasts, from above 5- or 6-sided, elongated, thin-walled, 50–95  $\times$  25–35  $\mu\text{m}$ , toward wings up to 107  $\times$  30  $\mu\text{m}$ , in transverse section (30.0–)37.5–47.5  $\mu\text{m}$  thick, occasionally with round oil body, 25–35  $\mu\text{m}$ , almost filling cell; marginal cells somewhat thicker-walled, especially on the outer side, in 1 or 2 rows (Figure 9E), elongated, 30.0–50.0  $\times$  12.5–15.0  $\mu\text{m}$ , inner cells 25–50  $\times$  25  $\mu\text{m}$ ; air pores (Figure 9F) very slightly raised, simple, oval, small, 17.5  $\times$  8.0  $\mu\text{m}$  and 125–250  $\mu\text{m}$  distant from each other, surrounded by 3 concentric rings of (6–)7–9 cells in each, innermost ring  $\pm 5$   $\mu\text{m}$  wide, with cells collapsed, in the next ring cells rounded to transversely oval or bluntly triangular, 12.5–17.5  $\times$  22.5  $\mu\text{m}$ , partly overlying outer ring of bluntly triangular or polygonal cells, 15–27  $\times$  35–40  $\mu\text{m}$ ; assimilation tissue (150–)250–320  $\mu\text{m}$  thick over

midrib, air chambers medianly in several vertical storeys, toward margins sloping obliquely, small and irregularly shaped, (25–)35–50  $\mu\text{m}$  wide, mostly empty and only rarely with 1 or 2 cells jutting into a chamber immediately below an air pore (Figure 9G), bounding cells oval to round, 45.0–52.5  $\times$  27.5–37.5  $\mu\text{m}$ , occasionally containing an oil body; storage tissue 450–650  $\mu\text{m}$  thick over midrib, thinning out gradually and absent at margins, cells angular and closely packed, 25.0–37.5(–40.0)  $\mu\text{m}$  wide, becoming somewhat smaller lower down, walls thick, porate and sometimes with a network of striations; rhizoids in clumps, mostly smooth, 22.5–25.0  $\mu\text{m}$  wide, pegged ones 10.0–12.5  $\mu\text{m}$  wide. *Scales* hyaline or pink to purple-red, arranged in two forwardly directed ventral rows, one on each side of midrib, not extending to margins of thallus, except at apex, obliquely crescentic with large, ovate or roughly triangular appendage (Figure 9H), (850–)1050–1200  $\times$  420–500  $\mu\text{m}$ , cells long-hexagonal, 92–150  $\times$  55–62  $\mu\text{m}$ , at apex ending in single cell forming an apiculus, 65–100  $\times$  15  $\mu\text{m}$ , at base constricted where joined to rest of scale, 1000–1100  $\times$  950–1050  $\mu\text{m}$ , where cells smaller and elongated, 60–100  $\times$  35–42  $\mu\text{m}$ , scale continuing into long tail,  $\pm 1200 \times 200$   $\mu\text{m}$ , cells 105–137(–220)  $\times$  (12–)22–25  $\mu\text{m}$ ,  $\pm 9$  cells per scale, only 42–55  $\times$  42–47  $\mu\text{m}$ , containing an oil body in each.

*Autoicous*. *Androecia* in raised cushions, oval or elongated or heart-shaped, 1.0–3.5  $\times$  1.0 mm, extending backwards from apex of main branch, frequently on apical or latero-ventral innovation, antheridia immersed and opening above via conspicuous papillae. *Archegoniophores* proximal to apical notch of main branch, single, occasionally paired at apices of two forking branches,  $\pm$  sessile when young and surrounded by up to 70 purple paleae, not arching over disc. *Carpocephala* at maturity raised on stalk, arising  $\pm 2$  mm back from apex of branch



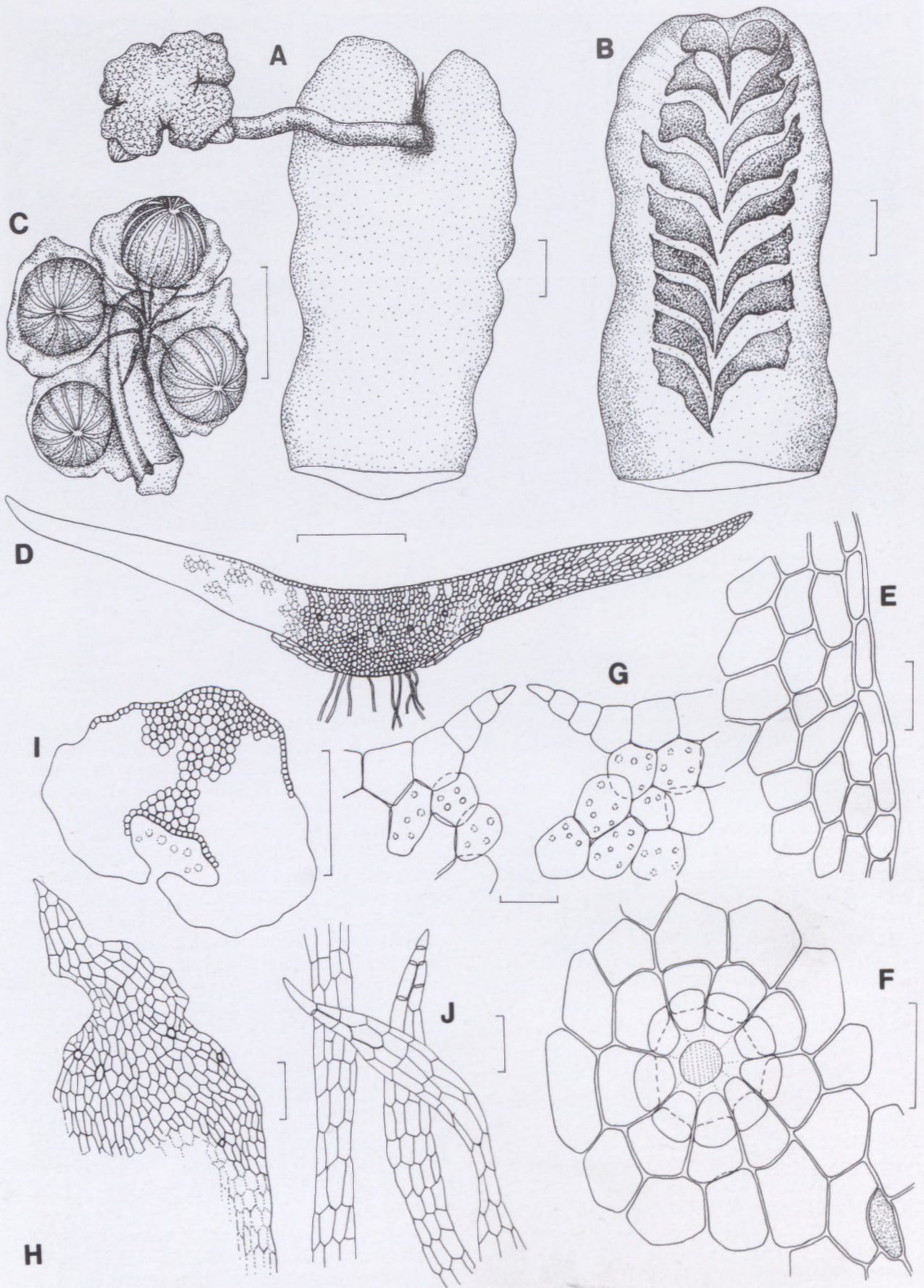


FIGURE 9.—*Asterella wilmsii*. A, dorsal face of thallus with stalk and carpocephalum; B, ventral face of thallus; C, carpocephalum from below; D, transverse section of thallus; E, marginal cells; F, air pore, dorsal cells and oil cell from above; G, transverse section of air pore and air chamber; H, ventral scale; I, transverse section of stalk; J, paleae from summit of stalk. A, I, J, S.M. Perold 2632; B, C, H. Anderson, 1219a; D, E, Perold & Koekemoer 2836; F, G, H, Perold & Koekemoer 2830. Scale bars: A–D, 1 mm; E–G, 50  $\mu$ m; H, I, 250  $\mu$ m; J, 100  $\mu$ m.



in apical notch, its length variable, (2-)4-10(-20) mm long, often purple, widening toward base, in transverse section at  $\pm$  midlength (Figure 9I)  $600 \times 525 \mu\text{m}$ , with rhizoidal furrow  $\pm 75 \times 100 \mu\text{m}$ , cortical cells in a single layer, thick-walled, especially on outside, rounded,  $15.0-27.5 \times 12.5 \mu\text{m}$ , medullary cells with thinner walls, but thickened at corners, up to  $37.5 \times 30.0 \mu\text{m}$ , at summit of stalk and also protruding from notches of disc, dark purple paleae (Figure 9J), occasionally pink or colourless, length variable, up to  $2000 \mu\text{m}$  long, rarely as much as  $3250 \mu\text{m}$  long, but then narrower, and only 3 cell rows wide, mostly up to 7 cell rows or  $\pm 325 \mu\text{m}$  wide at base, cells (4-)5 or 6-sided,  $\pm 155.0 \times 62.5 \mu\text{m}$ , gradually tapering to conical apical cell,  $100 \times 25 \mu\text{m}$ ; disc rounded, 3.5-5.0 mm across when bearing full complement of 4 or 5 capsules (Figure 9C), but sometimes only 1 or 2 capsules present and then smaller and asymmetric, above almost smooth or with low papillae further down, from which compound air pores lead to air chambers below; capsules spherical, wall with cells 4-6-sided,  $57.5-85.0 \times 42.5-65.0 \mu\text{m}$ , thin-walled and lacking spiral thickenings, but toward dehiscence line cells much thickened at corners, turning brown,  $27.5-47.5 \times 27.5-32.5 \mu\text{m}$ ; pseudoperianth extending up to  $1500 \mu\text{m}$  beyond involucre, generally with 16 segments, white or purple-stained,  $2250 \times 500 \mu\text{m}$ , tapering to narrow tip where coherent with other segments, cells  $100.0-137.5 \times 40 \mu\text{m}$ , toward tip  $62.5-75.0 \times 27.5-37.5 \mu\text{m}$ . Spores  $115.0-152.5 \mu\text{m}$  in diameter, triangular-globular, mostly yellow, translucent, wing thin, somewhat scalloped,  $20.0-22.5 \mu\text{m}$  wide, margin crenulate, distal face (Figure 10A, B) convex, with network of 5-8,  $\pm$  smooth, angular, complete or incomplete areolae across and extending over wing to margin on both sides,  $25-30 \times 20-25 \mu\text{m}$ , small subsidiary areolae sometimes present (Figure 10C), and extending over crests of main ridges,  $7.5-10.0 \mu\text{m}$  high; proximal face with prominent triradiate

ridge (Figure 10D, E), its arms up to  $25 \mu\text{m}$  high and continuous from the pole across wing to margin, each of 3 facets with rounded areolae, up to  $20 \times 20 \mu\text{m}$ , some with small, subsidiary areolae, others appearing smooth and hollowed out. Elaters (Figure 10F)  $225-230 \mu\text{m}$  long,  $17.5 \mu\text{m}$  wide in centre, slightly tapering to ends,  $12.5 \mu\text{m}$  wide, sometimes branched, doubly spiral, yellow. Chromosome number: not known.

#### DISCUSSION

*Asterella wilmsii* is the largest of the southern African species in this genus. It can also be distinguished from the others by the single, ovate or roughly triangular, large-celled appendage of the ventral scales, by the distinctly lobed disc of the carpocephalum, with purple paleae protruding from the notches and by the paleae being generally slightly broader based (up to 7 cells wide). The young, almost sessile archegoniophore is surrounded by purple paleae, which do not arch over it, as in *A. bachmannii*. The disc is less papillose and the spores are not as highly ornamented as those of *A. bachmannii*, often lacking smaller subsidiary areolae in the large areolae, which then appear to be almost smooth and hollow and extend across the wing. *A. wilmsii* is not as widespread in southern Africa as *A. bachmannii* and it is far less frequently collected. It is known from the PWV, Northern and Eastern Transvaal, Swaziland and KwaZulu/Natal (Figure 3). Its range extends northward into Zimbabwe (Coates Palgrave 2524; Eyles 414, 786, CH 1175; Henkel 2558; Miller CH 4249; Schelpe 4063, 5650; Volk 00640), from where it has also been reported by Best (1990), and into Angola (the type specimen of *A. angolensis*) as well as Malawi (Bizot *et al.* 1976). It may also grow in Zaïre, a tentative conclusion based on the ovate scale appendages

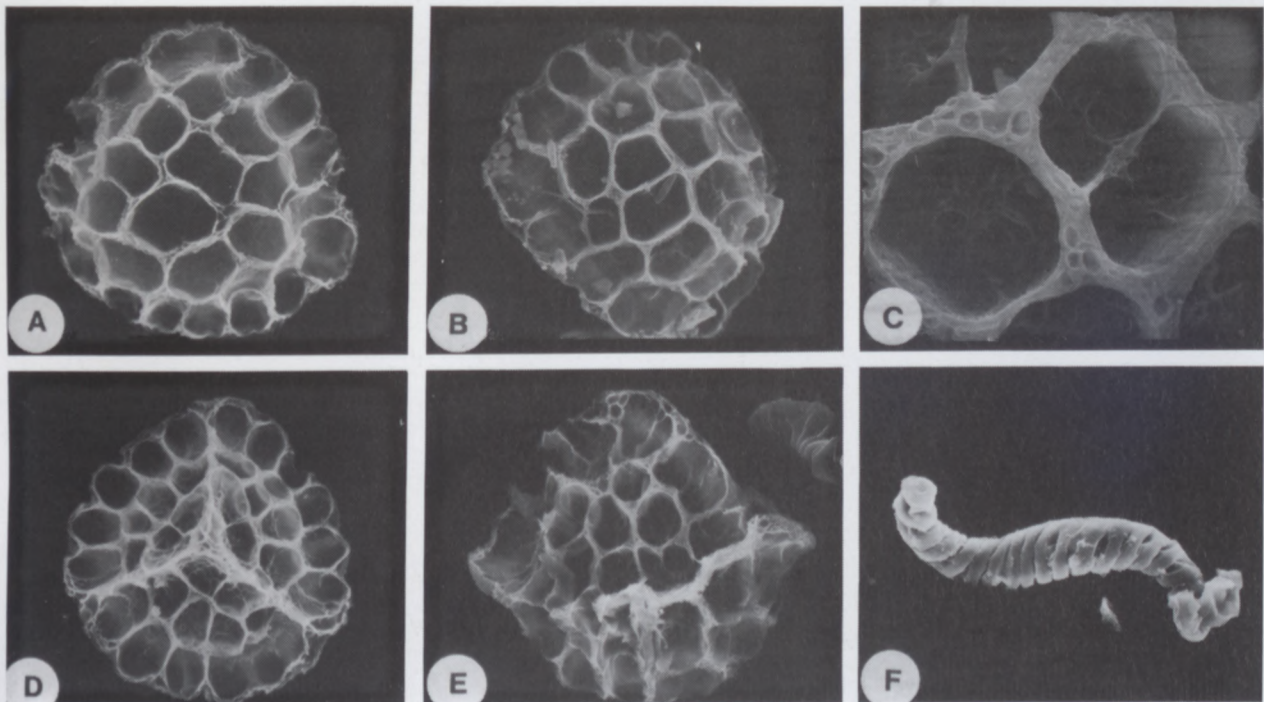


FIGURE 10.—SEM micrographs of *Asterella wilmsii*. A-E, spore: A, distal face; B, distal face seen from the side; C, much enlarged areolae on distal face, with some inner subsidiary areolae which also extend over their crests; D, proximal face; E, side view. F, elater. A, *Sim* CH 1269; B, *Doidge* 3187; C, *Sim* CH 1274; E, F, *Perold & Koekemoer* 2836. A, B,  $\times 316$ ; C,  $\times 1033$ ; D,  $\times 277$ ; E, F,  $\times 340$ .



illustrated by Vanden Berghen (1972) in his fig. 74H, I and the distal spore face in fig. 74K, which suggest this species, although the material was merely designated as *Asterella* sp. by him. *Asterella wilmsii* was also reported from Mozambique by Arnell (1963). The main distribution pattern along the mountains of the eastern part of the sub-continent suggests that it is an Afromontane species with isolated western outliers. It grows on damp soil along streambanks and waterfalls, sometimes in forested areas, forming dense mats, occasionally in association with *A. bachmannii* and *Symphogyna* spp.

Two specimens of *A. wilmsii*, Collins 775 from Rustenburg Kloof, and Eyles CH 1175 from Goromanzi in Zimbabwe, had been misidentified and reported by Arnell (1963) as *Reboulia haemispherica*. The presence of the genus *Reboulia* has not been confirmed in southern Africa and the species should accordingly be deleted from the checklist of southern African bryophytes (Magill & Schelpe 1979), as well as from *Plants of southern Africa: names and distribution* (Arnold & De Wet 1993).

#### SPECIMENS EXAMINED

*Alheit* 54610 (3) BOL. *H. Anderson* CH 1219 (2), 1219a (4), 1248 (1), 1262, CH 4504, CH 4505 (2), CH 12758 (4), CH 13288, CH 13587 (2) PRE. Arnell 46, 206, 216, 239, 267, 505, 5359 (3) BOL.

*Bachmann*, G13866 (lectotype), G13867 (2). *G. Bayer* CH 1235 (2) PRE. *Bews* CH 1229 (4), CH 1259, CH 1272 (2) PRE. *Bosman* CH 208, LI 3185 (2) PRE. *Bottomley* CH 172 (2), CH 263 (3), CH 1217, CH 2863 (4) PRE. *Bottomley & Doidge* CH 3565 (2), CH 3591 (4) PRE. *Braun* 714 (2) PRE.

*Coates Palgrave* 2524 (4) BOL. *Collins* 775 (4) PRE. *Condy* 13 (1), 14, 17 (2) PRE.

*Deal & Killick* 78b (2) PRE. *Dieterlen* 793a & b (1), 794, 1119, 1120, 1142 (2) PRE. *Doidge* CH 17 (2), CH 170 n.p., CH 3187 (4) PRE. *Du Plessis* 54613 (2) BOL. *Dyer* 863 (3) PRE.

*Edwards* CH 1270 (4) PRE. *Ellis* CH 13472 (1) PRE. *Eyles* 414 (4) CH 776 (2), 786 (4) 932, 933 (1), CH 1122 (2), CH 1175 (4) CH 1240, CH 1276, CH 1421 (2) PRE.

*Garabedian* CH 1218 (3), CH 1537 (2) PRE. *Garside* 6131, 6509, 6511, 6585 (3) BOL. *Gilliland* 215 (2) PRE. *Glen* 1674, 1675 (4) 1776, 2150, 2155, 2260, 2422, 2423, 2424, 2425, 3003, 3004, 3125 (2) PRE. *Glen & Reid* 1724 (1) PRE.

*Hardy* 930 (4) PRE. *Hardy et al.* 5377C (2) PRE. *Hean* 3660 (1) PRE. *Hendry* 9 (2) PRE. *Henkel* CH 762, 2558 (4) PRE. *Hepburn* CH 1262 (2) PRE.

*Jacot Guillarmod* CH 3673 (2) PRE. *Junod* 794 (2) PRE.

*Koekemoer* 106 (2), 284a, 295, 316, 318, 757, 869 (3), 974 (4) PRE. *Kresfelder* CH 163 (4) PRE.

*Leighton* CH 1216 (2) PRE. *Liebenberg* CH 2851 (4) PRE.

*Magill* 6370 (2) PRE. *Malan* 54611 (3) BOL. *Marais* 832 (1) PRE. *Michell* 8 (3) PRE. *Miller* CH 4249 (4), CH 4250 (2), 7869 (1) PRE. *Mogg* CH 158, CH 197, CH 1191, CH 1192, 4227, 4624 (2), 12557, 37642 (4) PRE. *Mohle* 315 (4) PRE. *Morley* 287, 297, 309 (3) PRE. *Mott* 861 (1) PRE.

*Newton* 25a (4) G.

*Obermeyer* TM 1940c, CH 3110 (4) PRE. *Oliver* 1474 (3) BOL. 7762 (2), 8854, 8877 (3) PRE.

*Pegler* 1356, 2150 (2) PRE. *S.M. Perold* 98, 100, 258 (2), 494, 509, 521, 522, 531, 610, 635, 646 (3), 685 (4) 686, 863 (2), 1457, 1603, 1899, 1909, 1934, 1992, 1997, 2040a, 2387, 2418 (3), 2482, 2487, 2488, 2572 (2), 2632, 2633 (4) 2703 (2), 2787, 2789 (3), 2800 (1), 2979, 2986 (1), 2986a, 3000 (2), 3001 (1) PRE. *Perold & Koekemoer* 2825 (2), 2830a, 2836 (4) 2848, 2855, 2856 (2), 2874 (4) 2877, 2898 (2), 2911 (4) 2913 (2), 2914 (4) 2916, 2917, 2919 (2), 2921 (4) 2934, 2946, 2947, 2951, 2960, 2968 (1), 2970, 2971 (2), 3030 (3) PRE. *Phelan* 375 (2) PRE. *Pieterse* 16 (3) PRE. *Pillans* 3991 (3) BOL. PRE.

*Reid* 969, 1012 (1) PRE.

*Schelpe* 2043, 4009 (2), 4063 (4) 4735, 4918a (3), 5255 (1) BOL. 5359 (2) PRE. 5650 (4) 6028 (2) BOL. 7729, 7792, 8045 (3) BOL. *Scott* 24 (2) PRE. *Sim. T.R.* CH 1160, CH 1198 (2), CH 1205 (4) CH 1206, CH 1208, CH 1210, CH 1213, CH 1215 (2), CH 1224 (4) CH 1226, CH 1239, CH 1244, CH 1245, CH 1246, CH 1247, CH 1248, CH 1250 (2), CH 1251 (4) CH 1252, CH 1254, CH 1455 (2), CH 1260 (3), CH 1263, CH 1265, CH 1268 (2), CH 1269, CH 1273, CH 1274 (4) CH 1297, 8147 (2) PRE. *Smook* 6422, 8237 (1) PRE. *Stirton* 8967 (4) 8992 (2), 9116 (3) PRE. *Stoneman* CH 1219 (2) PRE. *Symons* 8247 (2) PRE.

*Thomas* CH 947, CH 948 (2), CH 2869 (3) PRE.

*University Durban-Westville* 46, 49, 50 (2) PRE.

*Van der Bijl* 3, CH 1202, CH 1207, CH 1227 (2) PRE. *Van der Merwe* CH 232 (4) PRE. *Van der Schijff* 5131, 5860 (4) PRE. *Van Rooy* 781 (2), 1088 (1), 1289, 1348 (2), 1389, 1630 (4) 1696, 1822, 1830 (1), 2461 (2), 2716, 2930 (1), 3134, 3139 (2), 3144, 3580, 3609 (1) PRE. *Van Vuuren* 1476 (4) PRE. *C.M. Van Wyk* 2561 (3) PRE. *Veltman & Potgieter* 15 (4) 134 (2) PRE. *Venter* 8611 (2) PRE. *Vlok* 2675 (3) PRE. *Volk* 00640 (4) *Herb. Volk* 84/651 (1) M. PRE.

*Wagener* CH 13241 (2) PRE. *Wager Bequest* CH 250, CH 251 (2), CH 3691 (3), CH 3806 (4) PRE. *West* CH 3667 (2) PRE. *Wilms* G 1664 (1), G 001666 (lectotype), 02458 (1), G 024590 (4) G.

(*Eyles* 932, 933 and *Miller* 7869 are from Zimbabwe)

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