

Studies in the Marchantiales (Hepaticae) from southern Africa. 4. *Mannia capensis*, section and subgenus *Xeromannia* (Aytoniaceae)

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ABSTRACT

A taxonomic account of the genus, *Mannia*, and its only local representative, *M. capensis*, together with its distribution in southern Africa as currently known, is given. *Mannia capensis* var. *pallida* S.W. Arnell is not recognized here as a distinct variety, since the 'sulphuric yellow' spores by which Arnell (1963) segregated it, can be ascribed to immaturity.

UITTREKSEL

'n Taksonomiese verslag oor die genus *Mannia* en die enigste plaaslike verteenwoordiger, *M. capensis*, saam met die verspreiding daarvan in Suider-Afrika soos tans bekend, word gegee. *Mannia capensis* var. *pallida* S.W. Arnell word nie hier as 'n egte variëteit erken nie, aangesien die 'swawel-geel' spore, waarvolgens Arnell (1963) dit afgesonder het, bloot aan onvolwassenheid toegeskryf kan word.

***Mannia* Opiz** in Corda, Genera hepaticarum. Beiträge zur Naturgeschichte 12: 646 (1829); Frye & L. Clark: 60 (1937); R. Schust.: 601 (1953); D. Shimizu & S. Hatt.: 60 (1953); S.W. Arnell: 267 (1956); S.W. Arnell: 71 (1963). Type species: *M. raddii* Opiz = *M. triandra* (Scop.) Grolle.

Grimaldia Raddi: 356 (1818); Steph.: 792 (1898); Howe: 40 (1899); Evans: 43 (1923); Sim: 21 (1926). Type species: *G. dichotoma* Raddi, nom. illeg.

Synonymy partly after Grolle: 56 (1983a).

Thalloid, smallish to medium-sized, firm, compact and somewhat leathery to lacunose dorsally, linear or strap-shaped, bright green fresh, turning grey in older, dead parts, margins black; in crowded patches, on shallow soil covering rocky outcrops in exposed or somewhat sheltered niches, xerophytic.

Branches simple, or once, rarely twice pseudo-dichotomously branched, occasionally with latero-ventral or apical innovations; thickened over midrib, gradually thinning laterally into wings; apex entire, black tips of scale appendages reflexed over it; not grooved. *Dorsal epidermis* hyaline, cell walls thin to thickened, trigones present; air pores simple, inconspicuous, slightly raised, with 3 concentric rings of cells, their walls thin, leading below into small air chambers, these storied, mostly not containing chlorophyllose filaments; oil cells present; storage tissue up to twice (or more times) thicker than assimilation tissue above; ventrally reddish black; rhizoids some smooth, others pegged; ventral scales in one row on either side of midrib, red-black, large, obliquely triangular or semilunate with 1 or 2 linear-lanceolate appendages, not constricted at base, with a few scattered, colourless oil cells.

Dioicous, rarely monoicous, when gametangia on different branches. *Antheridia* immersed in rows along centre of branches with projecting conical papillae turning purple. *Carpocephala* terminal, arising from apical notch and raised on stalk with single rhizoidal furrow, disk apically domed to low conical, not lobed, continuous with campanulate involucre, each with protruding spherical capsule, dehiscing by discrete apical lid, the wall lacking annular thickenings. *Spores* with convex distal face bearing conspicuous hemispherical bullae, wing thick and undulating, proximal face on raised platform, with low triradiate mark; elaters tapering, 2- or 3-spiral.

***Mannia capensis* (Steph.) S.W. Arnell**, in Mitteilungen der Botanischen Staatssammlung, München 16: 263; S.W. Arnell 72: (1963); O.H. Volk: 233 (1979). Type: Bloemfontein, leg. *Rehmann* (G, holo.!).

Thallus smallish to medium-sized, linear or strap-shaped, occasionally jointed, firm and compact, older parts rarely somewhat lacunose, bright green fresh, sometimes on exposure to strong sunlight, becoming reddish or bronzed, especially toward margins, speckled with numerous small, slightly raised stomata, boundaries of narrow air chambers below faintly visible from above, not grooved, flat to slightly concave dorsally, margins with black borders narrow distally, but gradually widening proximally, somewhat scalloped, apically with cluster of shiny, reddish black, lanceolate scale appendages reflexed over edge when wet (Figure 1A); flanks black and shiny, transversely slightly wrinkled, tightly incurved and meeting along middle above dorsal face, becoming almost tubular, and partly exposing closely imbricate ventral scales with forwardly directed, oblique appendages, when dry; in crowded patches, simple or once, rarely twice, pseudo-dichotomously branched, sometimes with ventral innovations emerging laterally or from apical V-shaped sinus. *Branches* with total length up to 12 mm, terminal segments 3–7 mm long, closely to widely divergent, 2–4 mm

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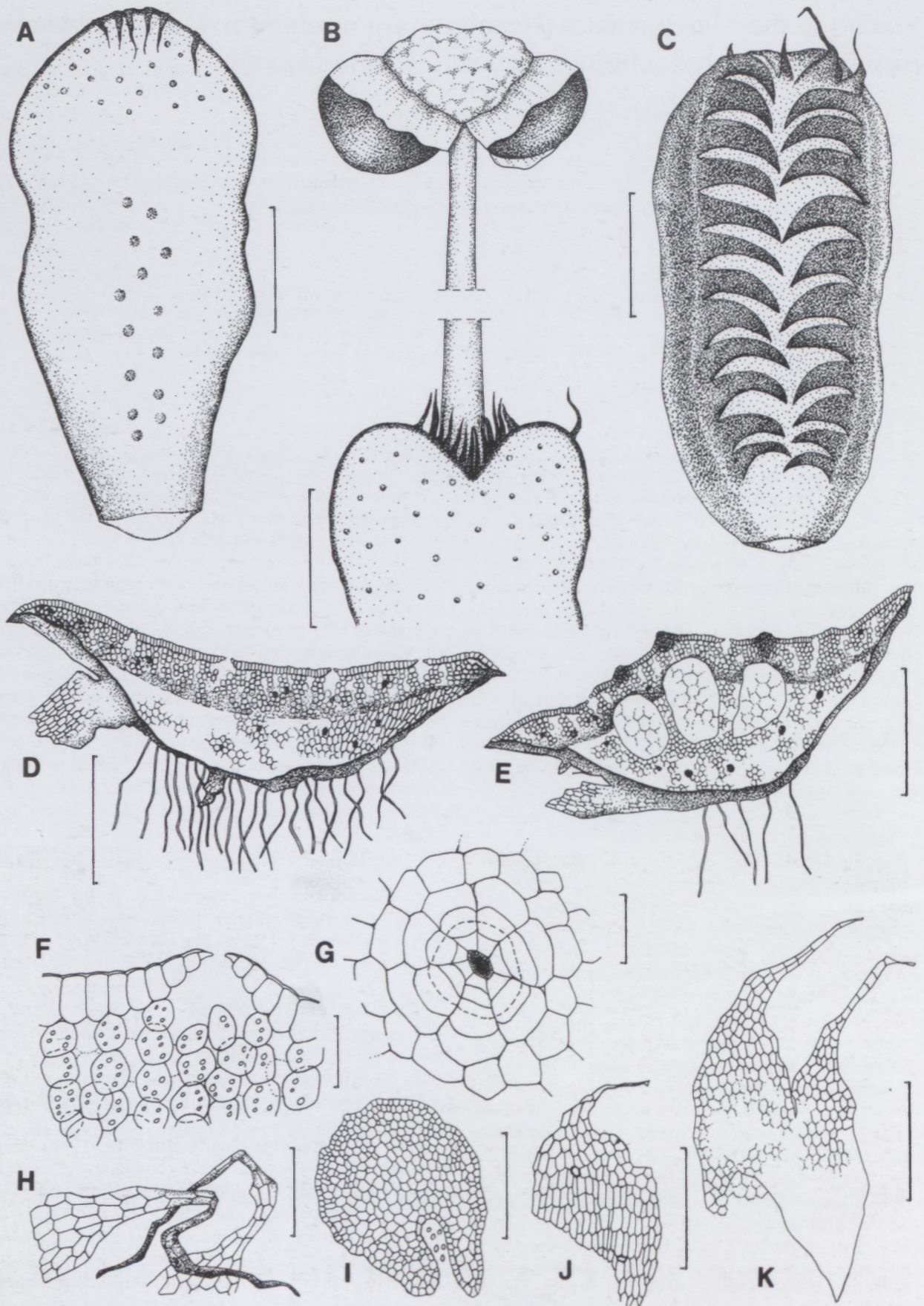


FIGURE 1.—*Mannia capensis*. A, dorsal aspect of male thallus with rows of antheridia; B, apical portion of female thallus with stalk arising from apical sinus and interrupted further up, at its tip bearing unlobed archegoniophore, involucre partly covering 2 capsules; C, ventral aspect of thallus showing scales; D, transverse section of thallus; E, transverse section of male thallus through antheridia; F, transverse section of air pore, dorsal cells, and assimilation tissue; G, air pore and dorsal cells from above; H, scales from foot of stalk; I, transverse section of stalk; J, ventral scale with one appendage; K, ventral scale with two appendages. A–D, G–I, K, *Glen 2117*; E, F–J, *Koekemoer 637*. Scale bars: A–C, 1 mm; D, E, 500 μ m; F, G, 50 μ m; H, I, 250 μ m; J, K, 500 μ m. Drawings by A. Pienaar.

wide, 525–775 μm thick over midrib, laterally thinning out into wings (Figure 1D); apex entire, hidden by reflexed appendages of distalmost ventral scales; margins acute, dorsally black or bronze-black along edge, ventrally entirely black, flanks sloping obliquely upward and outward; ventral face medianly broadly keeled, black, on either side of midrib a row of imbricate, obliquely directed reddish black scales with appendages (Figure 1C). *Dorsal epidermal cells* unistratose, hyaline, from above somewhat polygonal, 27–30 \times 15–25 μm , covered with minute spicules, trigones conspicuous but not bulging, in transverse section closely packed, rectangular, 30.0–37.5 \times 15.0 μm ; marginal cells purple-black, isodiametric, 20 \times 20 μm , or rectangular, 27 \times 15 μm , 2 or 3 rows wide, row at edge with outer wall convex, trigones lacking; air pores slightly raised, simple, oval or rounded, up to 25 \times 15 μm , (88–) 100–200 μm distant from each other, bounded by 3 concentric rings of cells, the radial walls not thickened: innermost row, the remains of a collapsed cell ring, usually numbering 7 flattened cells, trapezoidal in shape, 10 μm long, inner wall 5 μm wide, outer wall 10 μm wide, next row generally composed of 8 cells, transversely ovate, \pm 12.5 \times 15.0 μm , partly overlying outer row of somewhat curved, larger cells, \pm 30 \times 32 μm (Figure 1G); assimilation tissue 200–250 μm thick in transverse section, air chambers in several layers, medianly vertically storeyed, toward margins obliquely sloping, densely crowded, small, especially the lower ones, incompletely bounded by uniseriate walls consisting of cells mostly 17.5 \times 12.5 μm , and in uppermost layer, below air pore, with a few erect chlorophyllose filaments, the top cell of which conical, up to 37 \times 15 μm , those below rounded, 22 \times 25 μm , containing numerous chloroplasts, otherwise almost impossible to distinguish between bounding cells and those forming filaments (Figure 1F); storage tissue 300–

500 μm thick, cells angular, 6- or 7-sided, 40–62 μm wide; oil bodies solitary, scattered throughout thallus, almost entirely filling cell, \pm 67 \times 37 μm ; rhizoids arising from ventral epidermis, some smooth, up to 32 μm wide, others pegged, only 10 μm wide. *Scales* ventral, in 2 longitudinal rows, one on either side of midrib, black to reddish black, obliquely triangular or semilunate, with concave base, imbricate, large, body of scale \pm 600 \times 600 μm , cells rectangular, (35–)52–62 \times 17 μm , walls straight or slightly sinuous, bearing 1 (Figure 1J) or 2 (Figure 1K) (rarely 3), forwardly directed, linear-lanceolate appendages, not reaching thallus margins, except at apex, up to \pm 110 μm long, 17.5 μm or 5 cells wide below, tapering to single cell width toward apex, cells 32–40 \times 15–17 μm , remains of oil cells scattered, clear, round, 20 \times 30 μm , margins entire, occasionally with a few mucilage papillae.

Dioicous (rarely monoicous, but gametangia on different branches). *Androecia* consisting of up to 4 rows of conical papillae, 100 μm high, acropetally arranged along centre of branches (Figure 1A), green when young, turning purple with age, each with opening leading into immersed antheridial cavity below (Figure 1E). *Gynoecea* terminal, emerging knob-like from V-shaped, apical sinus and surrounded by numerous, arched, dark purple lanceolate scales up to 1150 μm long, narrowing from 4–6 cells wide at base to one cell wide at apex (Figure 1H), stalk eventually 5–25 mm long, cylindrical, 400 μm in diameter, irregularly ovate in transverse section, with single rhizoidal furrow (Figure 1I), only a few scales carried along and also present, but obscured at top of stalk, where joined to carpocephalum, the latter 2 mm across, straw-coloured, domed to low conical, papillose centrally (with compound pores), not or scarcely lobed, continuous with (1–)2–4 in-

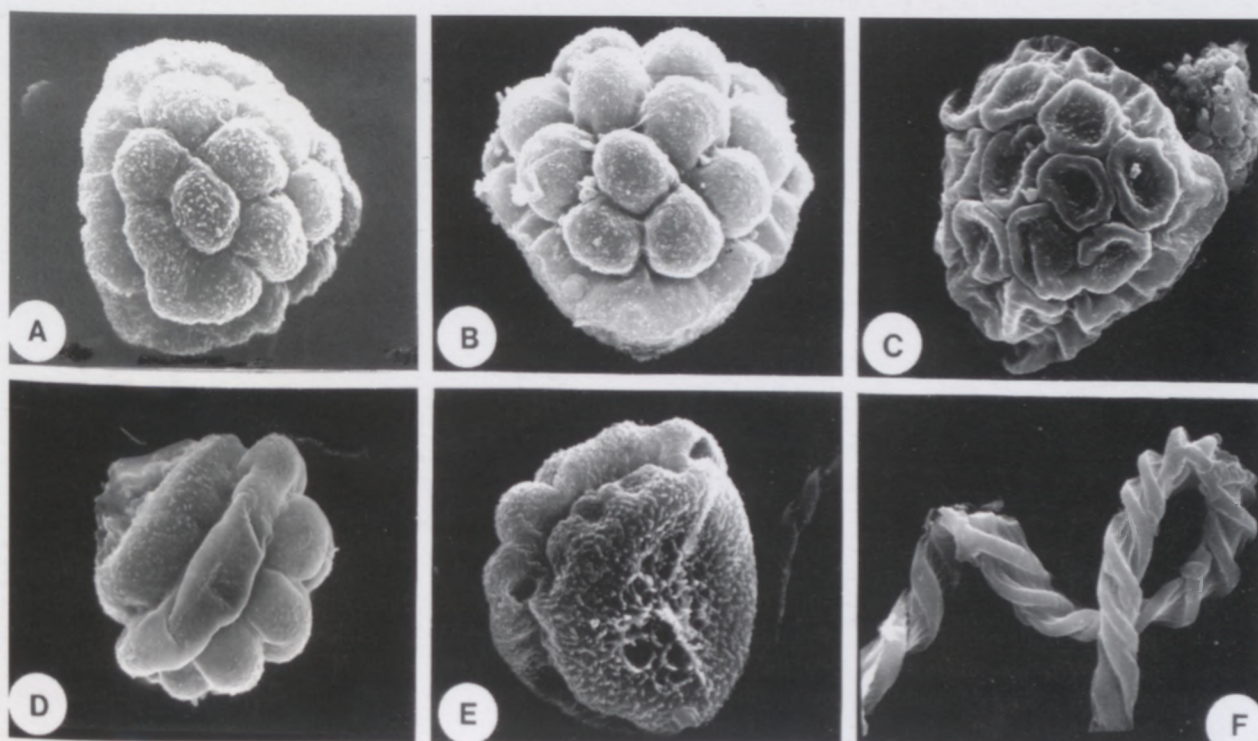


FIGURE 2.—*Mannia capensis*. SEM micrographs of spores and elater. A, distal face of spore; B, distal face of spore slightly tilted; C, distal face of 'yellow' spore; D, spore seen from side; E, proximal face of spore; F, elater. A, E, Eyles CH 1179; B, Bosman 199; C, F, Volk 00828; D, Burrows 2521. A, E, \times 540; B, D, \times 480; C, \times 570; F, \times 740.

volucres, these membranous, wide-mouthed and bell-shaped, each with single, protruding, globular, dark brown capsule (Figure 1B), the wall with 4–6-sided cells, $27\text{--}62 \times 37 \mu\text{m}$, lacking annular thickenings and dehiscing along row of smaller cells, $37 \times 27 \mu\text{m}$, forming a well-defined lid. Spores $75\text{--}80 \mu\text{m}$ in diameter, polar, roughly triangular-globular, light brown, semitransparent, with distal face convex (Figure 2A, B), bearing 10–13 crowded and very conspicuous, hemispherical bullae, $\pm 22 \mu\text{m}$ wide, mostly well separated from each other, occasionally 1 or 2 collapsed; wing lighter, straw-coloured, $7.5 \mu\text{m}$ wide, porate at each of 3 angles (or in between as well), wavy and undulating, inflated and twisted in side view (Figure 2D); proximal face with raised base, triradiate mark present but weak (Figure 2E), slightly raised or not, arms not extending to edge, with shallow, crowded and overlying areolae in centre, both faces generally covered with granules. Elaters reddish brown, tapering toward ends, $212\text{--}275 \mu\text{m}$ long, $12.5 \mu\text{m}$ wide in centre, $7.5 \mu\text{m}$ wide at tips, 2–3-spiral (Figure 2F). Chromosome number: $n = 9$ (Bornefeld 1987).

Mannia is said by Schuster (1992) to be a relatively large genus with ± 18 species worldwide, but Engel (1990) says that there are only six species. All of them, except *M. capensis*, are from the northern hemisphere. The species are generally distinguished from each other by the size of the plants, the compactness of the assimilation tissue, the colour and size of the scales and their appendages and by the dorsal cells of the thallus, whether they are thin- or thick-walled, whether the epidermis remains intact and leathery, or regularly becomes lacunose on ageing and whether the plants are aromatic or not. *Mannia capensis* has spores which, in morphology, are closely similar to those of the American *M. californica*, but in the latter species they are purple in colour. Two subfamilies are recognized in the Aytoniaceae, Aytonioideae and Reboulioideae. In southern Africa the latter comprises the genera *Asterella*, *Cryptomitrium* and *Mannia*.

The genus was originally known as *Grimaldia* Raddi, but the specimen on which it was based, contained two elements. Evans (1938) showed that the name, *Grimaldia*, is illegitimate and recently Grolle (1983b) submitted a proposal to conserve the name, *Mannia* Opiz (1829), against *Cyathophora* S.F. Gray (1821). Two subgenera are recognized by Grolle (1976): *Mannia* and *Arnelliella*, with the former having two sections, *Mannia* and *Sindonisce*; *M. capensis* was placed by him in section *Mannia*. Later on, after the introduction of the new version of Article 10, ICBN (Voss *et al.* 1983), Grolle (1983c) changed this grouping as follows:

subgenus *Mannia* (subgenus) *Arnelliella* (Mass.) Grolle, with section *Neesiella* (Schiffn.) D. Shimizu & S. Hatt.
subgenus *Xeromannia* Grolle with sections *Xeromannia* and *Sindonisce*.

The two species, *M. fragrans* and *M. androgyna* (the latter selected as the type of subgenus *Xeromannia*), are classified in section *Xeromannia*. They are closest to *M. capensis* and therefore, it too is placed in section *Xeromannia*, subgenus *Xeromannia*.

Schuster (1956, 1992) is, however, convinced that the division of *Mannia* into subgenera, based largely on the form of the aerenchyma tissue 'compact' versus 'loose', is artificial. He concluded that it 'is perhaps an artifact based on environmentally induced distinctions' (Schuster 1956). Furthermore, Schuster (1992) (and others) regard the air chambers as lacking chlorophyllose filaments, stating that 'secondary walls are largely incomplete, their free margins are usually irregular, or even produced as short teeth, which may give the superficial impression of representing 'free photosynthetic filaments', as illustrated in Figure 1F of this study.

Grolle (pers. comm.) suspects that *M. capensis* could be conspecific with *M. androgyna*. From the few authentically named specimens of *M. androgyna* examined for this study, it is difficult to come to a definite decision about this, although its spore ornamentation is very similar to that of *M. capensis*. The dorsal epidermal cells in *M. androgyna*, described by Müller (1951–1958) as having delicate walls, appear to be somewhat thicker-walled and yellowish, the width of the pigmented margins of the thalli is greater, it is generally a larger plant and the scale appendages extend beyond the thallus margins, particularly the distal ones. Live plants of *M. androgyna* were unfortunately not available for cultivation and comparative study with *M. capensis*.

Fertile plants of *M. capensis* can be distinguished quite readily from other members of the Marchantiales by the stalked, domed and unlobed carpocephala, lacking a pseudoperianth. Sterile specimens are more difficult to distinguish, particularly from *Targionia hypophylla* and small *Asterella* plants. In *T. hypophylla*, however, the dorsal air pores are larger, and, when dry, white-encircled; in *Asterella* species, with the exception of *A. muscicola*, the air pores and air chambers are generally difficult to detect from above, wet or dry.

Although not common, *Mannia capensis* has been collected over a wide area in southern Africa. It is known from Namibia, western, central and eastern Transvaal, Orange Free State, northern, central, western and southern Cape Province, as well as from Zimbabwe (Best 1990) (Figure 3). Bizot & Pócs (1982) reported its occurrence in East Africa on the Uluguru Mountains, as disjunct. Here

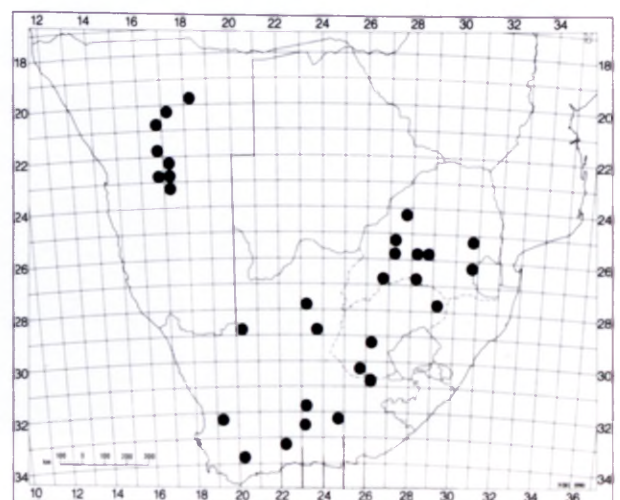


FIGURE 3.—Distribution of *Mannia capensis* in southern Africa.

too, it grows in open, exposed sites. Otherwise it is found in rocky clefts or on shallow soil covering granite, quartzite, sandstone or sometimes dolomite, occasionally in association with other liverworts such as *Riccia* spp. and *Plagiochasma* spp. At Kogmanskloof, near Montagu in the Cape, it grew together with *Exormotheca pustulosa*. It is a pronounced xerophyte, with the storage tissue thicker than the assimilation tissue.

Arnell (1963) described a new variety from Kogmanskloof, *M. capensis* var. *pallida*, on the basis of its sulphuric yellow spores. These spores, as remarked by Garside (note found with specimen Arnell 798, (BOL 54675)), were, however, only immature. Garside further noted that 'the bullae of the spore coat were also open at the apex—perhaps by mounting in glycerine, they had burst. I saw Dr Arnell's preparation (at Sea Point where he stayed)'. Signed 'S.G.' In a specimen, Volk 00828, collected at Okahandja, Namibia, two capsules were borne in the same carpocephalum: one contained bright yellow spores whereas the other had the usual brownish spores. The ornamentation of the yellow spores was less well-formed, with the papillae low or collapsed (Figure 2C) and sometimes confluent; that of the brown spores was as described above, thus furnishing clear proof for Garside's statement, that the yellow colour of the spores must be ascribed to immaturity and does not justify varietal status. *Mannia capensis* var. *pallida* S.W. Arnell is accordingly not recognized here as a distinct variety.

SPECIMENS EXAMINED

NAMIBIA.—1918 (Grootfontein): Ossa, around shaly base of rocks, (–CA), Volk 81/147 (M, PRE). 2016 (Otjiwarongo): 7 km S of Otjiwarongo, prominent granite hill near road, on soil in shade of boulders, (–DA), *Brusse* 4206 (PRE). 2017 (Waterberg): ETO 98 Oros, Fels, schattig, (–AA), Volk 00452 (M). 2116 (Okahandja): Okahandja OK 206, auf Granit, (–DD), Volk 00828 (M). 2216 (Otjimbingwe): L WIN 329, Matchless Mine, Glimmerfelstrip, (–DB), Volk 006771 (M). 2217 (Windhoek): Neudamm, Glimmerschiefer, Überhänge am Rivier, (–AD), Volk 00685, 00686 (M); 10 km östlich Kl. Windhoek, Glimmerschiefer, Überhang, (–CA), Volk 00905 (M); Bellerode, Glimmerschiefer, Überhang, (–CA), Volk 86-879a, 86-880 (M); WIN 63 Glimmerschiefer, Überhänge schattig, in Rasen, (–CB), Volk 00948 (BOL, M); Voigtland, Klipp-Kamp, an Felsen, (–CB), Volk 11400 (BOL, M). 2317 (Rehoboth): REH 20, Güllschau, auf Granit, (–AC), Volk 6104 (M).

TRANSVAAL.—2427 (Thabazimbi): Sterkstroom 250 KO farm, on top of koppie between farmhouse and R517 road between Vaalwater and Ellisras, on soil overlying Waterberg sandstone, (–BD), *Glen* 2114, 2117 (PRE). 2527 (Rustenburg): Pilanesberg Nat. Park, along new road between main road and Mankwe loop, 1.0–1.5 km from main road, on humus-rich soil over white felsite, (–AC), *Glen* 2461, 2466 (PRE); Rustenburg, 14 km N of, on road to Northam, on soil over granite outcrops, (–CA), *S.M. Perold* 227 (PRE); Magaliesberg, Rietfontein Farm, Hamerkop Kloof, on streambank on humus-rich soil overlying quartzite, (–CD), *Glen* 3176 (PRE). 2528 (Pretoria): Pretoria, Wonderboom, (–CA), *Bosman* CH 199 (PRE), *Bottomley* BOL 54667 (BOL); Hennops River Valley, (–CA), *Meeuse* 9621 (BOL, PRE); Magaliesberg Range, 18 km W from Lanseria Airport, Plover's Lake Farm (owner Everard Read), up the hill, (–DD), *Condy* 46 (PRE). 2530 (Lydenburg): 15 miles NE of Lydenburg (–BA), *Schelpé* 5906 (BOL); Sudwala Caves, between boulders on path between Dinosaur Park and cave entrance, (–BC), *Koekemoer* 637a (PRE); Sudwala Caves, ± 30 km NW of Nelspruit, on earth bank next to path leading to Dinosaur Park, (–BC), *S.M. Perold* 402 (PRE). 2626 (Klerksdorp): Klerksdorp, (–DC), *Sister Victoria* 273 (PRE). 2628 (Johannesburg): Kuilfontein Farm, 10 miles SE of Heidelberg, quartzite rock, acid, sandy soil, (–CB), *Mogg* 37590 (PRE). 2630 (Carolina): Kangwane, Songimuelo Game Res., Farm Kortegin 168 IT, on soil along flat granite outcrop, (–BB), *Smook* 8236a (PRE).

O.F.S.—2729 (Volksrust): 42 km SE of Vrede on road to Verkykerskop, Farm Drie Kop at Aasvoëlkop, on ground between boulders on steep slope above stream, (–CB), *Smook* 6422a (PRE). 2926

(Bloemfontein): Bloemfontein, Wilde Als Kloof, (–AA), *Potts* CH 1178 (PRE); Bloemfontein, Eagle's Nest, (–AA), *Potts* CH 1266 (PRE); Bloemfontein Botanical Garden, uncultivated part on hill, (–AA), Volk 81/062 (BOL, M, PRE). 3025 (Colesberg): 4 miles S of Trompsburg, around base of boulders, S aspect, (–BB), *Schelpé* 5282 (BOL). 3026 (Aliwal North): 12 km SE of Bethulie, Cliftonvale Farm, Albert Dist., foot of rocky cliffs at seepage zone, (–CA), *H.H. Burrows* 2521 (PRE).

CAPE.—2723 (Kuruman): just east of Bretby Mine, in damp rock crevices and under overhanging rocks in kloof, (–CA), *Oliver* 1450 (BOL). 2820 (Kakamas): Augrabies, Granit Felssockel Überhang, (–CB) Volk 00554 (M). 2823 (Griekwastad): 32 miles east from Griquatown, in seasonally wet limestone crevices, (–DC), *Schelpé* 5884 (BOL). 3123 (Victoria West): Three Sisters, (–CC), *Schelpé* 5830 (BOL). 3219 (Wuppertal): Clanwilliam Dist., Farm Mertenhof, Bidouw Valley, on slope facing east below a Bushman Cave, (–AA), *Oliver* 1465 (BOL). 3224 (Graaff-Reinet): Naudesberg Pass, 40 km N of Graaff-Reinet, at seepage at large vertical rocks at roadside, on soil, (–BA), *S.M. Perold* 947 (PRE). 3320 (Montagu): Kogmanskloof, (–CC), *S. Arnell* 791, 795, 798 (BOL). 3322 (Oudtshoorn): Swartberge, First River, Nordseite, Uferböschung, (–AC), *Lübenau-Nestlé* SA 122 (PRE).

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