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Studies in the Marchantiales (Hepaticae) from southern Africa. 1. The genus *Dumortiera* and *D. hirsuta*; the genus *Lunularia* and *L. cruciata*

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Keywords: *Dumortiera*, *D. hirsuta*, Dumortieroideae, Hepaticae, *Lunularia*, *L. cruciata*, Lunulariaceae, Marchantiaceae, Marchantiales, taxonomy, southern Africa, Wiesnerellaceae

ABSTRACT

The genera *Dumortiera* (Dumortieroideae, Marchantiaceae) and *Lunularia* (Lunulariaceae), are briefly discussed. Each genus is represented in southern Africa by only one subcosmopolitan species, *D. hirsuta* (Swartz) Nees and *L. cruciata* (L.) Dum. ex Lindberg respectively.

UITTREKSEL

Die genusse *Dumortiera* (Dumortieroideae, Marchantiaceae) en *Lunularia* (Lunulariaceae) word kortliks bespreek. In suidelike Afrika word elke genus verteenwoordig deur slegs een halfkosmopolitiese spesie, *D. hirsuta* (Swartz) Nees en *L. cruciata* (L.) Dum. ex Lindberg onderskeidelik.

DUMORTIERA Nees

Dumortiera *Nees ab Esenbeck* in Reinwardt, Blume & Nees ab Esenbeck, Hepaticae Javanicae, Nova Acta Academiae Caesareae Leopoldina-Carolinae Germanicae Naturae Curiosorum XII: 410 (1824); Gottsche *et al.*: 542 (1846); Schiffner: 35 (1893); Stephani: 222 (1899); Sim: 25 (1926); Müller: 394 (1951–1958); S. Arnell: 52 (1963); Hässel de Menéndez: 182 (1963). Type species: *Dumortiera hirsuta* (Swartz) Nees.

Synonymy according to Nelson & Parnell: 35 (1992):

Hygropyla Taylor: 390 (1836).

Hygrophila Taylor (orth. var.) in Mackay: 53 (1836) non R. Br. (1810).

Hygrophyla Taylor (orth. var.) in Mackay: X (1836).

Hygropila Taylor (orth. var.) in J.D. Hooker & T. Taylor: 576 (1844).

Askepos Griffith 2: 340 (1849).

Thallus, large, flat and thin, dark green, in overlying patches; on shaded, damp soil or on wet rocks. Branches with apical innovations or dichotomously furcate, occasionally lateral, moderately divergent, thickened over midrib, wings gradually thinning toward margins; apex emarginate.

Dorsal epidermis very thin-walled, temporary, vestigial, air pores absent, air chambers mostly reduced to 1- or 2-celled vestiges, reported rarely to have reduced chlorophyllose filaments, cells containing numerous fairly large chloroplasts; storage tissue compact, confined to ventral part of midrib; oil cells rare, each with a single, large oil body; rhizoids along midrib and ventrally appressed against wings, mostly smooth, occasionally tuberculate; scales ventral over midrib, vestigial and evanescent.

Monoicous or dioicous. *Antheridia* sunken in subsessile disciform receptacles, which are fringed with bristles and borne singly at apex of thallus on short bifurrowed stalk. *Archegonia* in groups of 8–16 in saccate, fleshy involucres, on lower surface of 6–8-lobed disciform receptacle with marginal sinuses dorsally, raised on stalk with two rhizoidal furrows; after fertilization and maturation, each involucre generally containing a single sporophyte consisting of foot, seta and capsule; capsule wall unistratose, with annular thickenings, dehiscing irregularly. *Spores* small, papillose. *Elaters* slender, tapering, 1–3-spirate. *Gemmae* absent.

Dumortiera hirsuta *(Swartz) Nees* in Reinwardt, Blume & Nees ab Esenbeck, Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum XII: 410 (1824); Gottsche *et al.*: 542 (1846); Spruce: 566 (1885); Stephani: 224 (1899); Macvicar: 41 (1926); Sim: 25 (1926); Müller: 396 (1951); S. Arnell: 52 (1963); Hässel de Menéndez: 182 (1963). Type: Jamaica, leg. *Swartz s.n.* [S, holo.!; MW, iso. (Hb. Hoffm. No. 8497); UPS, fide Grolle 1976].

Marchantia hirsuta Swartz: 145 (1788).

M. irrigua Wilson ex Hooker in Smith: 106 (1833). *Hygropyla irrigua* (Wilson) Taylor: 390 (1836); Mackay: 54 (1836); Stephani: 150 (1899). *Dumortiera irrigua* (Wilson) Nees: 159 (1838). *D. hirsuta* var. *irrigua* (Taylor) Spruce: 566 (1885). Type: Ireland, Turk Cascade, near Killarney, *Mr Wilson*.

D. hirsuta var. *angustior* Gottsche, Lindenberg & Nees: 544 (1846).

D. hirsuta var. *intermedia* Gottsche, Lindenberg & Nees: 544 (1846).

D. velutina Schiffner: 256 (1893).

Askepos brevipes Griffith: 340 (1849). Type: India, in sylvis umbrosis Tingrei agri, II 1836.

Thallus hygrophyllous, large and creeping, broadly and rather irregularly strap-shaped, uniformly dark green, translucent, thin and flat, but often marginally undulate, wet (Figure 1A); crisped and shrivelled, dull, unable to survive dry; in crowded, overlying patches, once to several times dichotomously or occasionally laterally furcate or

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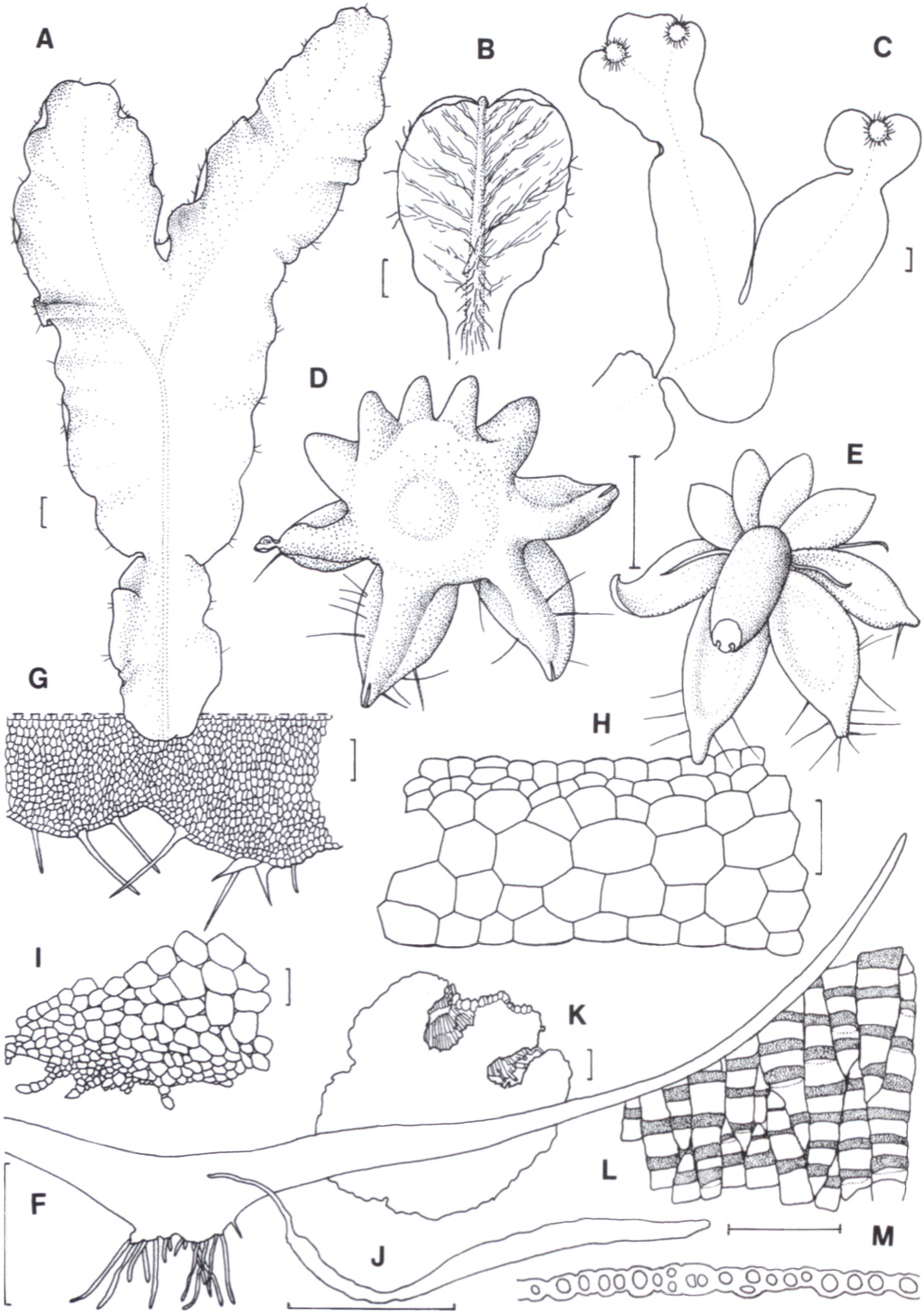

FIGURE 1.—*Dumortiera hirsuta*. A, dorsal view of thallus; B, ventral view of thallus; C, male plant with disciform receptacles at apex; D, young female receptacle seen from above; E, young female receptacle seen from below; F, transverse section of thallus; G, margin of thallus with hairs; H, transverse section of thallus, much enlarged; I, lower cells of costa and vestigial scales in transverse section; J, filiform scale from top of stalk; K, transverse section of stalk with two rhizoidal furrows; L, capsule wall cells with thickenings; M, transverse section of capsule wall. A, F–H, *S.M. Perold 2694*; B, *S.M. Perold 2634*; C, *Nicholas 1176*; D, E, I, *H. Anderson CH 13495*; J–L, *Doidge CH 3581*. Scale bars: A–C = 2 mm; D–F, J = 1 mm; G, K = 100 μm; H, I, L, M = 50 μm. Illustrations by G. Condy.

with apical innovations; branches 50–95 × 8–13(–22) mm and ± 500 μm thick over median, ventrally bulging midrib (also visible from above), laterally gradually thinning out into wide wings (Figure 1F); apex shortly emarginate; margins undulate, occasionally scalloped, sparsely hirsute, hairs ± 250.0 μm long, ± 12.5 μm wide at base, tapering slightly to somewhat blunt tip (Figure 1G).

Epidermis, pores and air chambers absent; dorsal cells from above, 4–6-sided, variable in shape and size, 27–57 × (17–)22–32 μm, in cross section ± 15 μm thick, containing chloroplasts; marginal cells thin-walled, long- or short-rectangular, 25–62 × 12–20 μm; midrib with ± 18 rows of cells of which upper 3 rows larger, rounded, up to 100 × 137 μm, with somewhat wavy walls and scattered chloroplasts, lower group of cells angular, smaller, ± 30 μm wide, lacking chloroplasts; wings medianly with 3 rows of large cells, decreasing in number to one row at margin, covered by dorsal and ventral layer of smaller chlorophyllose cells; oil bodies quite rare, for the most part confined to scattered cells in the midrib, yellow-brown, elongate or round, ± 40 μm across; rhizoids below midrib numerous, mostly smooth, 15–20 μm wide, occasionally tuberculate, 5 μm wide, also in widely spaced, arching strands below wings, radiating toward margins and appressed to ventral face of wings (Figure 1B) or scattered; ventral scales hyaline, vestigial (Figure 1I), without appendages, evanescent, only near apex.

Monoicous or dioicous. *Antheridiophore* subsessile, disciform, 2.75 mm in diameter, 0.6 mm thick in centre, flattening toward sides, containing antheridia, 470 × 250 μm, ± ovate, acropetally arranged, but not in radiating rows, sunken into disc, borne singly at apical notch of thallus (Figures 1C; 2A) on very short, 1 mm diameter, bifurrowed stalk, with rhizoids lining furrows; hyaline, filiform scales on ventral face of disc, the latter encircled by dense outer fringe of bristle-like hairs, 600–1100 μm long, base 20–25 μm wide, a few scattered hairs dorsally. *Archegoniophore* disciform, 3.75 mm in diameter; dorsal face (Figure 1D) becoming radially grooved by sinuses; ventral face 6–8-lobed (Figure 1E) in radiating rows and then almost star-shaped, sparingly bristled; archegonia in groups of 8–16, enclosed in green, fleshy, saccate involucres, long archegonial necks protruding through narrow slit-like apical openings; receptacle eventually raised on stalk arising at apical notch of thallus between overlapping sides, ± 40 mm long and ± 925 μm wide, cortical cells ± 15.0 × 12.5 μm, inner cells ± 50 × 30 μm; along its length 2 furrows lined with rhizoids (Figure 1K) and its top (where joined to disc) encircled by numerous filiform, hyaline scales (Figure 1J), up to 3750 μm long and 300 μm wide at base, apex only ± 3 cells wide, cells mostly ± 125 × 22 μm; at maturity generally only one sporangium borne in each involucre, rarely two and quite often none, elliptical, 2.5 × 1.5 mm, supported on elongating seta and protruding from membranous calyptra, pseudoperianth lacking; capsule wall unistratose (Figure 1M) with annular or semi-annular thickenings (Figure 1L), dehiscing irregularly via longitudinal suture lines and releasing large numbers of elaters and spores (Figure 2B). *Spores* golden brown, semi-transparent, distal face rounded, proximal face ± flat to slightly peaked in the centre, triradiate mark indistinct, 25–30 μm across its longer axis, ornamented with numerous nodules or tubercles, irregular in size and shape (Figure 3A). *Elaters* yellow-brown or orange-brown, mostly with doubly spiral strands (Figure 3B), ends tapering, 225–470 × 7.5–10.0 μm in middle and 3.5 μm wide at tips. *Gemmae* absent.

Chromosome number: n = 9 (Berrie 1960, Bornefeld 1987); n = 18 (Tatuno 1941); n = 27 (Tatuno 1941, Berrie 1958). According to Tatuno (1938, 1939) the 9, 18 and 27 chromosome sets present different races with different distributions and edaphic ecology, but he considers them as belonging to the same species.

Only a few of the specimens examined were fertile; most of these were dioicous, with male and female receptacles borne on separate plants. Monoicous plants were quite rarely found, but have frequently been reported in the literature and even bisexual receptacles are known (Evans 1919).

All southern African specimens have been identified as belonging to *D. hirsuta*: the dorsal face of the thallus is always ± smooth and lacks papilliform cells or traces of air chambers. *D. nepalensis* and *D. velutina*, which our material resembles, are considered to belong to the polymorphic species *D. hirsuta* (Grolle & Piippo 1984). Arnell (1963) referred to material from southern Africa (Cape Province, Transvaal, Natal) as *D. hirsuta* var. *nepalensis*. Schuster (1992) considers *D. nepalensis* (Taylor) Nees to be a distinct taxon under the name of *D. hirsuta* subsp. *nepalensis* (Taylor) Schuster which is not found in Africa. *D. hirsuta* is subcosmopolitan and is widespread in tropical and temperate regions, generally growing in sheltered, wooded, shaded and damp areas, i.e. it is hygrophilous. In southern Africa it is known from northern and eastern Transvaal, Swaziland, Natal, Zululand and eastern, southern and southwestern Cape (Figure 4). Further northwards in Africa, *D. hirsuta* is reported from (or has been collected in) Zimbabwe (Best 1990), Zambia [*S.M. Perold 2670* (PRE)], East African Mountains (Arnell 1956), East Africa (Bizot *et al.* 1985), Tanzania, Malawi, Mozambique (Bizot & Pócs 1979), Rwanda and Burundi (Váňa *et al.* 1979).

On the basis of flavonoid data, Campbell *et al.* (1979) found chemical affinities between *Dumortiera* and *Wiesnerella*, suggesting that they belong in a common family, Wiesnerellaceae (Inoue 1976). This was accepted by Grolle (1983), but Schuster (1984) has retained *Dumortiera* in the Marchantiaceae, creating a new subfamily, Dumortieroideae Schust., for it and designating *Dumortiera* as the type genus. *Dumortiera* has also been classified in the Dumortieroideae by Bischler (1988), who regards *Dumortiera* and *Wiesnerella* as morphologically remotely related, although having similar flavonoid patterns. The treatment of Schuster (1984) is followed here, even though the phylogenetic position of *Dumortiera* remains a matter of some controversy, as conceded by Schuster (1984). Supporting the above treatment are terpene studies of the genera by Asakawa *et al.* (1979, 1980a, 1980b, 1981), who found that *Wiesnerella denudata* and *Conocephalum conicum* shared 17 of these terpene compounds, but only had three in common with *Dumortiera hirsuta*. Luteolin 5-O-glucuronide, the flavonoid shared by *Dumortiera* and *Wiesnerella* which was considered diagnostic for the Wiesnerellaceae by Campbell *et al.* (1979), has since also been

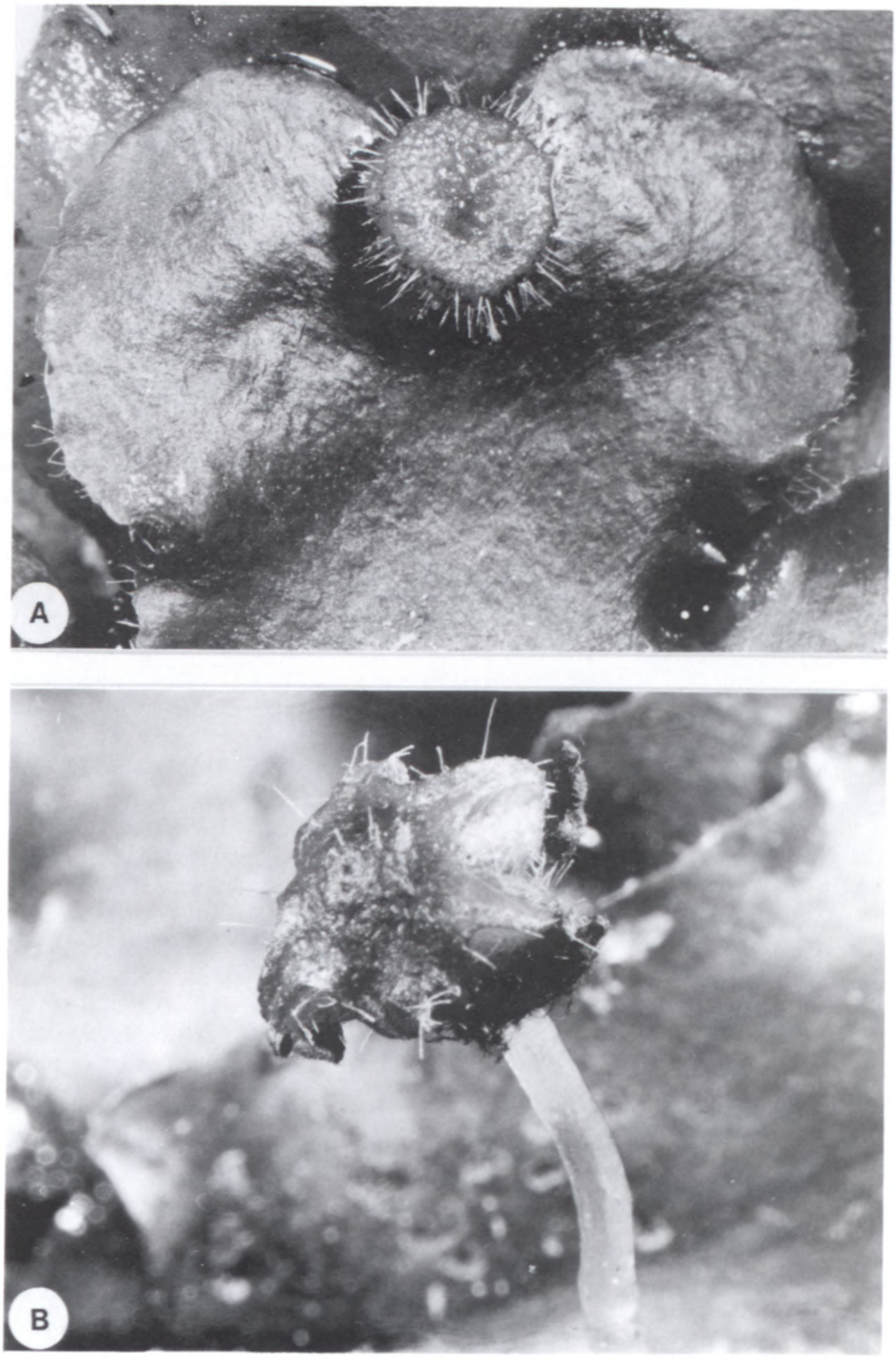

FIGURE 2.—*Dumortiera hirsuta*. A, male plant with subsessile antheridiophore from above; B, stalked archegoniophore with dehisced sporangia, front one releasing many spores and elaters. A, B, *Koekemoer 989*, × 9.

reported for *Conocephalum* by Porter (1981). Whittemore (1991) therefore cautions against drawing taxonomic conclusions from a small number of compounds.

SPECIMENS EXAMINED

TRANSVAAL.—2230 (Messina): Entabene, (–CC), *Bottomley* (PRE); Entabene, (–CC), *Schelpe 6020* (BOL); Soutpansberg, Entabene, (–CC), *Thomas 856* (PRE). 2329 (Pietersburg): Pietersburg, (–CD), *Van Vuuren 1469* (PRE); Haenertsburg, (–DD), *Putterill 3604* (PRE). 2330 (Tzaneen): Woodbush For. Res., Magoebaskloof, near stream, (–CC), *H. Anderson CH 13495, CH 13499* (PRE); *Bosman 3188*, (PRE); De Hoek For. Res., Debengeni Falls, on stream bank, beyond foot bridge, (–CC), *S.M. Perold 2634* (PRE); Woodbush, locally abundant in deep shade on streambank, (–CC), *Schelpe 6070* (BOL). 2331 (Phalaborwa): Letaba, (–DC), *Scheepers 984* (PRE). 2430 (Pilgrim's Rest): Farm Cyprus near Ofcolaco, in gorge named 'Terrible Hollow', (–AB), *H. Anderson CH 4527* (PRE); Mariepskop Forestry Water Works, on outside of watertank, also under overhang, dense shade, (–DB), *Vorster 87C* (PRE); Mariepskop, near dam in Klaserie River, montane forest, on rock against bank next to stream, in shade, (–DB), *Vorster 572*; Mariepskop For., Bedford footpath in forest on soil of streambed, full shade, (–DB), *Vorster 1398* (PRE); Mariepskop For., Blyde River footpath, on exposed tree root at streamside in forest shade, (–DB), *Vorster 1472* (PRE); Mariepskop, Blyde River footpath, hanging from vertical sandstone rocks in forest shade, (–DB), *Vorster 1473* (PRE); Mariepskop, Magalieskop Res. For., on damp earth bank, dense shade, (–DB), *Vorster 1815* (PRE); Mariepskop, (–DB), *Van der Schijff 4482* (PRE); Mariepskop, Klaserie River by dam, beneath rocks, (–DB), *Van der Schijff 6291* (PRE); Mount Sheba Nat. Res., at the 'Grotto', on dripping cliffs, forming extended mats on wet vertical rock face, (–DC), *Jacobsen 4421* (PRE); Mount Sheba Nature Reserve at the 'Grotto', on dripping rock cliffs, (–DC), *Perold & Koekemoer 2864* (PRE); Pilgrim's Rest, (–DD), *Van der Schijff 6367* (PRE). 2527 (Rustenburg): Nature Res. Cederbergkloof, near Utopia, (–CA), *Koekemoer 972* (PRE). 2530 (Lydenburg): Farm Klipsteen, between Lydenburg and Dullstroom, at waterfall, on rock, (–AB), *H. Anderson CH 13446* p.p. (PRE); Sabie, Lone Creek Falls, on soil near footpath, (–BA), *S.M. Perold 2694* (PRE); Sabie Gorge, (–BB), *V.A. Wager 21* (PRE); on road to Lydenburg, at turnoff to Witklip, Coromandel Farm, at waterfall, (–AB), *Perold & Koekemoer 2839, 2844* (PRE); Nelspruit Dist., Rooiwal, (–BC), *Bosman 3180* (PRE); Rosehaugh, (–BD), *T.R. Sim CH 1286* (PRE); Kaapsehoop, (–DB), *H.A. Wager 47* (PRE); Berlin State Forest, Kaapsehoop hiking trail near Battery Creek, (–DA), *Koekemoer 973, 975* (PRE).

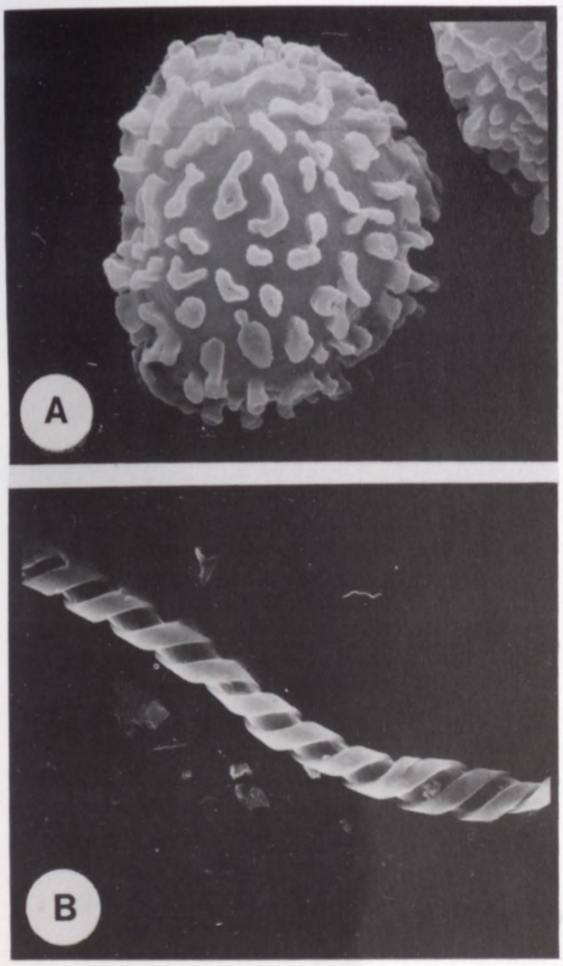

FIGURE 3.—*Dumortiera hirsuta*. A, spore, distal view; B, part of elater. A, B, *H. Anderson CH 4527*. A, × 1730; B, × 480. SEM micrographs by S.M. Perold.

SWAZILAND.—2531 (Komatipoort): King Forest, Havelock, occasionally on wet shaded earth bank in forest, (–CC), *Schelpe 6195* (BOL).

NATAL.—2731 (Louwsburg): Ngoma For., bank of river, (–CD), *Gerstner 4386* (PRE); Ngoma For., Cetshwayo waterfall walk, vertical slope, seepage, in deep shade, (–CD), *Glen 2881* (PRE); Ngoma For., along path in Ntendeka, alongside streams in forest interior, (–CD), *Nicholas 1176* (PRE); Ngoma Forest, occasionally on deeply shaded earth banks in forest, (–CD), *Schelpe 6237* (BOL); Ngoma For., (–CD), *T.R. Sim CH 1302* (PRE); Ngoma For., Ntendeka, in forest, (–CD), *A.E. van Wyk 6973* (PRE). 2828 (Bethlehem): Mont-aux-sources, (–DD), *Doidge 171* (BOL, PRE). 2831 (Nkandla): Nkandla Forest, common on rocks in and near water in shade, (–CA), *Nixon 57* (BOL); Eshowe, Signal Hill, (–CD), *Van der Plank CH 1290, CH 1298* (PRE); Ngoya, (–DC), *T.R. Sim CH 1289* (PRE). 2929 (Underberg): Mpendle Dist., 6 miles along Everglades/Boston Road River on stream bank, in shade, (–DB), *Moll 726* (BOL, PRE); Home Rule, Polela, (–DC), *T.R. Sim CH 1305* (PRE); Xumeni For., (–DD), *Doidge 3581* (PRE); Donnybrook, (–DD), *Scott 3756* (PRE). 2930 (Pietermaritzburg): Karkloof, (–AC), *T.R. Sim CH 1291* (PRE); Buccleugh, (–AD), *T.R. Sim CH 1301* (PRE); Pietermaritzburg, Town Bush, (–CB), *T.R. Sim 7523, 7534*; Waterfall, (–CB), *T.R. Sim 7548, 7574, 7586* (PRE); Pietermaritzburg, (–CB), *T.R. Sim 1296* (PRE); Sweetwater stream, (–CB), *T.R. Sim 1300* (PRE); Zwaartkop, (–CB), *T.R. Sim CH 1328* (PRE).

CAPE.—3226 (Fort Beaufort): Katberg For., (–BC), *Garabedian S.A.M.H. 49743* (BOL; PRE); Hogsback, (–DB), *T.R. Sim 1895; Van der Bijl 176; Young 1303* (PRE). 3227 (Stutterheim): Perie Forest, (–CC), *T.R. Sim 7534* (BOL). 3318 (Cape Town): Cape Town, (–CD), *H.A. Wager 28* (PRE). 3322 (Oudtshoorn): Rust en Vrede, at Oudtshoorn, (–CA), ex Herb. C. vanden Berghen (BOL). 3323 (Willowmore): Gouna Forest, near Lily vlei, (–CC), *S. Arnell 1736* (BOL); Bloukrans River Pass, at bridge in forest, on rocks along stream, (–DC), *Stirton 9648* (PRE); Bloukrans, along pass in river ravine, on vertical cliff face, (–DC), *Zantovska 155* (PRE). 3419 (Caledon): Oudebos, Rivier-sonder-end, (–BB), *Thorne 3617* (BOL, PRE). 3420 (Bredasdorp): Leeuwrivier Mountains, Swellendam, (–AB), *Stokoe 9486* (BOL). 3423 (Knysna): Knysna, Garden of Eden, (–AA), *S. Arnell 2096* (BOL); Knysna, (–AA), *T.R. Sim 1292* (PRE).

LUNULARIA Adanson

Lunularia *Adanson*, Familles des plantes 2: 15 (1763); Micheli: 4 (1729); Nees ab Esenbeck: 29 (1838); Gottsche *et al.*: 510 (1846); Schiffner: 35 (1893); Stephani: 216 (1899); Howe: 59 (1899); Macvicar: 38 (1926); Sim 123 (1926); Müller: 366 (1951–1958); S. Arnell: 73 (1963); Hässel de Menéndez: 125 (1963). Type species: *Lunularia cruciata* (L.) Dum. ex Lindb.

Selenia J. Hill: 120 (1773) nom. illeg.
Staurophora Willd. 3: 101 (1809).
Dichominum Neck.: 345 (1790) (as subgenus).
Marsilia O. Kuntze 2: 837 (1891).
Sedgwickia S. Bowdich: 35 (1825).

Thallus large, flat, somewhat glossy, green, in overlying patches, sometimes in extensive turfs; on damp soil in old gardens, nurseries and forested areas, may have been introduced into southern Africa. Branches dichotomously furcate toward apex, new growth by apical or lateral innovations; thickened over midrib, gradually thinning toward slightly undulate, hyaline margins; apex emarginate. Dorsal epidermis persistent, hyaline, cell walls sometimes thickened at corners or entirely; air pores simple, elevated and conspicuous, surrounded by several concentric rings of cells, leading below into individual air chambers, these in one layer and floored by chlorophyllose layer of 3–5-celled erect, branched filaments; storage tissue compact, cells colourless, sometimes with pitted walls; scattered cells throughout with single, large, brown oil body; rhizoids numerous, between ventral scales and on midrib, some smooth, others tuberculate; scales ventral, in curved parallel rows on either side of midrib, with round or reniform appendages, several cells containing oil bodies.

Dioicous. *Antheridia* sunken into slightly elevated, oval or kidney-shaped, disciform receptacles encircled by raised, membranous sheath, at sides of male thalli (although originally terminal). *Archegonia* enclosed in terminal receptacles, but by continued growth of thallus

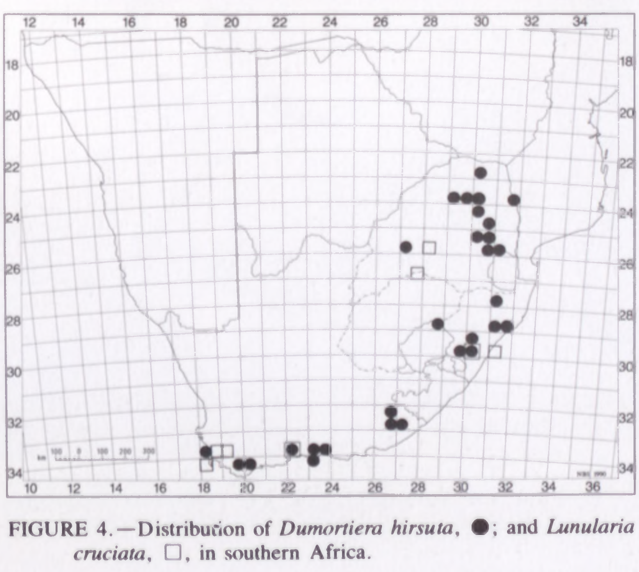

FIGURE 4.—Distribution of *Dumortiera hirsuta*, ●; and *Lunularia cruciata*, □, in southern Africa.

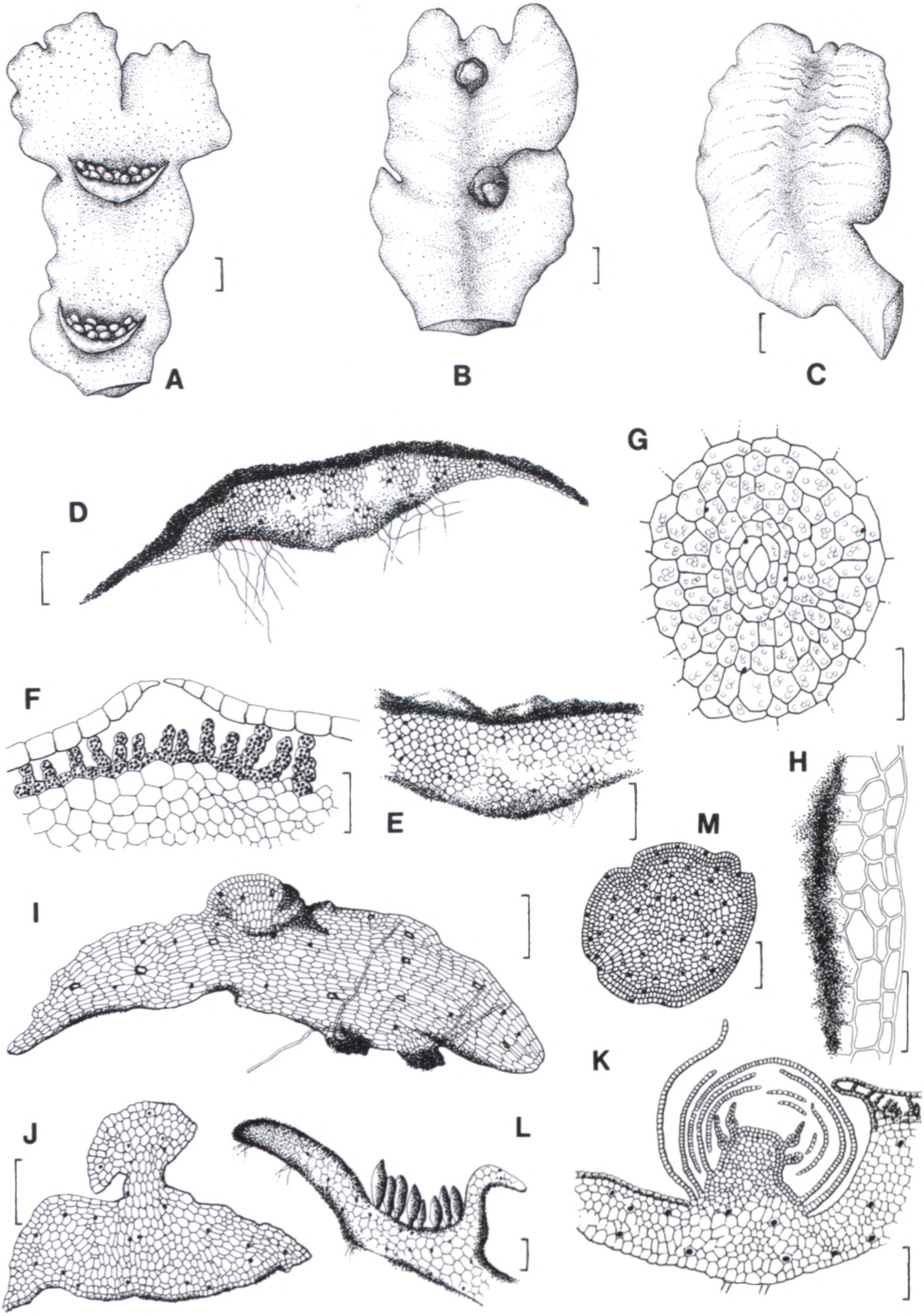

FIGURE 5.—*Lunularia cruciata*. A, dorsal view of thallus with gemma cups; B, female plant with young archegoniophores; C, ventral view of thallus with new lateral branch; D, transverse section of thallus; E, transverse section of midrib region, much enlarged; F, transverse section of air chamber; G, air pore seen from above; H, margin of thallus with hyaline cells, seen from above; I, older scale; J, young scale; K, longitudinal section through young archegoniophore; L, longitudinal section through gemma cup; M, gemma. A, D–H, J, L, M, *S.M. Perold 2821*; B, C, *S.M. Perold 1996*. Scale bars: A–C = 2 mm; D, E, K, L = 1 mm; I, J = 500 μm; F, M = 100 μm; G, H = 50 μm. Illustrations by A. Pienaar. Figure 1K partly after Benson-Evans & Hughes fig. 4.

laterally situated, conical, white and bud-like when young, sheathed in layers of scales and slightly sunken into rounded depression with distinct rim; after fertilization and further growth, four tubular involucres in the form of a cross are formed, each enclosing one or two sporophytes, composed of foot, seta and capsule, raised on unfurrowed, hairy stalk; capsules eventually exposed by elongation of seta, the wall unistratose, lacking annular thickenings, dehiscing by 4 valves. *Spores* very small, green or brown, smooth. *Elaters* long, tapering and bispiral. *Gemmae* numerous, disc-shaped, inside crescent-shaped ridge; wholly diagnostic. *Sporophyte* virtually unknown in southern Africa.

Lunularia cruciata *(L.) Dum. ex Lindberg*, Notiser Sällskap pro Fauna et Flora Fennica Förhandlingar 9: 298 (1868); Howe: 60 (1899); Macvicar: 40 (1926); Sim: 24 (1926); Müller: 366 (1951–1958); S. Arnell: 73 (1963); Hässel de Menéndez: 126 (1963); E.O. Campbell: 31 (1965). Type: In Europae umbrosis [OXF, syn.; H-SOL, isosyn., fide Grolle (1976)]. For detailed synonymy see K. Müller (1951–1958).

Thallus moderately large and flat, ribbon-like or margins somewhat irregular (Figure 5A), glossy, bright green to yellowish green, with outlines of subdorsal air chambers faintly visible from above, each of the polygonal areas with a central air pore, when wet; reticulum indistinct, leathery, when dry; in crowded overlying patches, dichotomously or irregularly furcate or with apical or lateral innovations from ventral side of thallus (Figure 5C). *Branches* 40–55 × 5–8(–10) mm, ± 650(–1000) μm thick over median, ventrally bulging midrib, gradually thinning out laterally into wide wings (Figure 5D); apex emarginate or sinusoidal; margins slightly undulate and somewhat scalloped, with outer 4(5) cell rows hyaline.

Dorsal epidermal cells hyaline, in one layer, 5- or 6-sided to irregular in shape, 35–50 × 20–30 μm, thin-walled to somewhat thicker-walled or only thickened at corners, in cross section 20–25 μm thick; marginal cells with outermost row short- to long-rectangular (Figure 5H), 15–27 × 10–12 μm, cells of inner rows polygonal, 17–27 × 25 μm; air pores simple, oval, raised, 17–25 × 12–20 μm in diameter, bordered by 3–5 rings of curved, smaller, thin-walled cells (Figure 5G), 7–12 × 17–27 μm, outer row of cells somewhat larger, 15–20 × 20–22 μm; air chambers with domed roof (Figure 5F) raised 37–52 μm above filaments, laterally separated by non-chlorophyllose unistratose partitions obscured by filaments, floored by dense chlorophyllose layer, ± 70 μm thick, of 3–5-celled erect, branched filaments, filled with chloroplasts, top cell often clavate, ± 20 × 15 μm, others 20 × 12 μm; midrib below assimilation cells, with ± 15(–20) rows of compact colourless storage cells (Figure 5E), 50–75 × 45–50 μm, becoming smaller ventrally, some with pitted walls, layers gradually decreasing in the wings; scattered cells with brown oil bodies, round or oval, 30 × 30–45 × 27 μm; ventral epidermal cells 30–40 μm wide, 15–25 μm thick in cross section; rhizoids on midrib between scales, numerous, smooth, ± 30 μm wide, tuberculate, (10–) 17–22 μm wide. *Scales* hyaline, some basal cells purple, on either side of midrib, stretched across ventral face of wings, near apex of thallus, base ± 1375 × 550 μm, with rounded, constricted appendage (Figure 5J), ± 400 × 250 μm; cells mostly polygonal, ± 65 × 25 μm, some smaller, with oil body 22 × 25 μm, almost entirely filling cell; older scales larger (Figure 5I), base up to 1000 × 4250 μm, appendage ± 600 μm wide.

Dioicous. Male plants quite rare in southern Africa. *Antheridiophore* on alternate sides, having originally developed in terminal sinus near apex (Figure 6A), slightly raised, ovate, flattish discs, 2–3 mm in diameter, encircled by membranous sheath with crenate edges, containing numerous antheridia, individually sunken in flask-shaped cavities (Figure 6B), opening above by pores. *Archegoniophore* originally also developing in terminal sinus near apex, with further growth of thallus leaving it behind, so that it appears lateral in position on alternate sides of thallus (Figure 5B); commences as domed disc ± 200 × 375 μm, bearing several archegonia in radiating rows and attached by very short stalk to floor of shallow, round hollow, 1100 μm wide × 300 μm deep, with crenate rim; sheathed in ± 3 layers of scales (Figure 5K), outer layer formed by fused, shaped scales, bulging in centre and constricted below and above, upper edge irregularly fringed with filiform cellular appendages of up to 7 rectangular cells, ± 35 × 15 μm, cells in body of scale thick-walled, 5- or 6-sided, up to 57 × 25 μm, in between numerous smaller cells, 4- or 5-sided, 25 × 15 μm, almost entirely filled with single oil body; between scales and especially from base of archegoniophore and arching over it, numerous uniseriate, long hairs of 16–20 cells each. Further development not recorded as fertilization did not take place, nor are sporophytes available for study. *Gemmae* numerous, disc-shaped (Figure 5M), notched

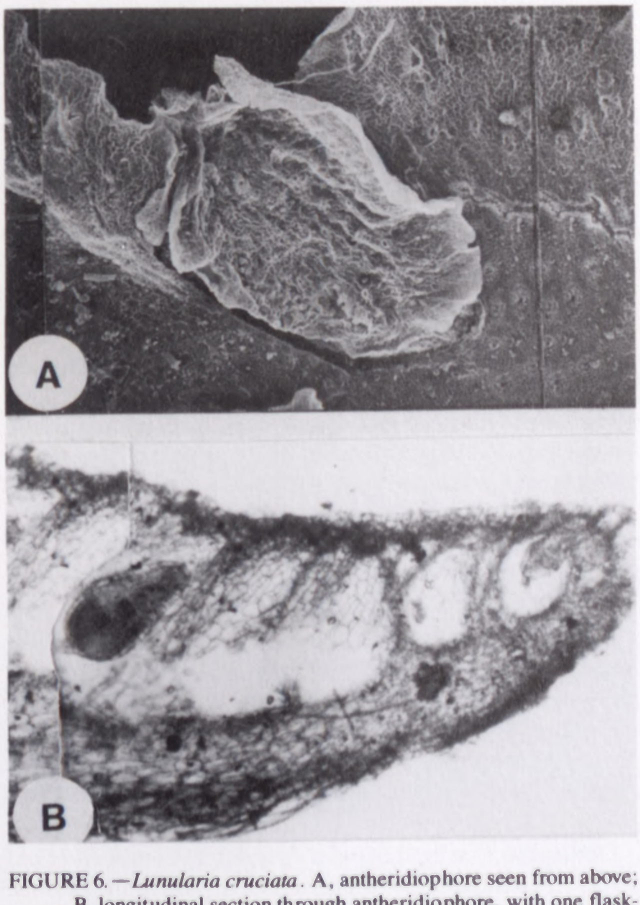

FIGURE 6.—*Lunularia cruciata*. A, antheridiophore seen from above; B, longitudinal section through antheridiophore, with one flask-shaped antheridium in place. A, *Wilman BOL. No. 24870*; B, *Koekemoer 1004*. A, × 22; B, × 38. A, SEM micrograph; B, LM photograph.

by 2 opposite, lateral growing points, ± 430 μm in diameter when mature, developing upright on short stalk, inside crescent-shaped cupule (Figure 5L), ± 3 mm wide with crenate to entire ridge on proximal side. *Chromosome number* n = 8 (Heitz 1927); n = 9 = 8 + x/y^2 (Lorbeer 1934); n = 9 (Bornefeld 1987).

DISCUSSION

As mentioned in the description, male plants with antheridial receptacles are exceedingly rare in southern Africa and the only two, *Wilman BOL No. 24870*, on loan from BOL and *Koekemoer 1004* (PRE), were received after completion of Figure 5 and therefore not illustrated there (see Figure 6). Male plants are so rarely seen, that Sim (1926) had categorically stated that they are not present in South Africa, but then added 'so far as is known'. He must have been unaware of Saxton's find. No female plants with fertilized archegonia and mature sporophytes were available for study; even plants with young archegoniophores are quite rare, judging both from personal experience and from the literature (Saxton 1931; Goodman 1956; E.O. Campbell 1965). Saxton (1931) found both male and female plants in Cape Town in 1908, but had to wait for almost 20 years for plants with mature archegoniophores (forwarded from Dartmouth, England) to complete his studies on the life history of *L. cruciata*. Giffen sent plants with young archegoniophores from Oranjezicht, Cape Town to Sim (Sim 1926) and Auret (as mentioned in Benson-Evans & Hughes 1954) reported the regular production of female branches in the vicinity of Johannesburg. Of my own collections, only *S.M. Perold 1996* from Devon Valley Hotel, Stellenbosch (November 1987), had young archegoniophores.

Since so many collections are from nurseries or city gardens, it would appear that *L. cruciata* may have been introduced into southern Africa. It is not frequently found here, most collections being from the southwestern Cape, a few from southern Transvaal and some from Natal, and then quite frequently from nurseries (Figure 4). Further north in Africa, *L. cruciata* is known from Zimbabwe (Best 1990), Malawi (Nyika Plateau, *S.M. Perold 2667, 2676* (PRE)); East African Mountains (Arnell 1956); Tanzania (Serengeti) (Vanden Berghen 1965); Uluguru Mountains, Rungwe Mountains (Bizot & Pócs 1979); Congo Rep. (Katanga) (Vanden Berghen 1965). Pócs (pers. comm.) states that in East Africa, *L. cruciata* is found in many natural habitats in the montane forest belt, mostly on young volcanoes such as Mt Elgon and Mt Meru and even on the Comoro Islands.

Lunularia cruciata is quite widespread in the southern hemisphere but regarded by Engel & Schuster (1982) as probably Laurasian in origin. Since sexual reproduction and subsequent spore production are so rare, its gemmae obviously present a highly effective means of ensuring its dispersal, which is most likely aided by human activities.

On the basis of its flavonoid chemistry, Campbell *et al.* (1979), include it in the Marchantiaceae, but in the present treatment Grolle (1983) is followed and *L. cruciata* is classified in the monotypic family, Lunulariaceae Klinggr. (1858).

Its phylogenetic position seems rather unclear, Schuster (1984b) arguing that he would place it 'low' in the Marchantiales on account of its high level of seta retention, 2–3 sporophytes per gynoecium and a capsule with 4 well-defined valves. On the other hand, he expresses the viewpoint (Schuster 1984b) that its archegoniophore, clearly formed from two dichotomies, each producing archegonia, is complex and therefore an advanced feature.

SPECIMENS EXAMINED

TRANSVAAL.—2528 (Pretoria): Pretoria, Union Buildings Nurseries, (–CA), *Bottomley CH 135* (PRE); Pretoria, National Botanical Institute Nurseries, (–CA), *S.M. Perold 2821* (PRE). 2627 (Potchefstroom), Vereeniging, (–DB), *T.R. Sim CH 1283* (PRE); Roodepoort, Sterlig Nursery, on gravel and brick walls of flowerbeds, (–DD), *Koekemoer 1004* (PRE).

NATAL.—2930 (Pietermaritzburg): Hilton Road, (–CB), *T.R. Sim CH 1279, CH 1280* (PRE). 2931 (Stanger): Durban, Silverglen Nurseries, (– CC), *S.M. Perold 2805* (PRE).

CAPE.—3318 (Cape Town): Kirstenbosch, (–CD), *S. Arnell 412* (BOL); Window Gorge, Table Mountain, (–CD), *S. Arnell 405* (BOL); Claremont Park, (–CD), *Garside 6653* (BOL); near Round House, (–CD), *Garside 6132* (BOL); Oranjezicht, (–CD), *Giffen CH 1281* (PRE); Glen Picnic Resort, just below Round House, Lion's Head, (–CD), *S.M. Perold 645* (PRE); Round House, Lion's Head, on soil beneath trees, (–CD), *S.M. Perold 650* (PRE); Newlands Forest, on soil under trees, (–CD), *S.M. Perold 662* (PRE); Cape Town, (–CD), *T.R. Sim CH 1278, CH 1282* (PRE); Skeleton Gorge, rock face, very wet forest, (–CD), *Stirton 9415* (PRE); mountain slopes above Kirstenbosch, (–CD), *Stokoe s.n.* (BOL); Kirstenbosch, (–CD), *Wilman 24870* (BOL); Stellenbosch, (–DD), *Burtt Davy CH 1277* (PRE); Pniel, on tree trunk mixed with moss, (–DD), *Morley 314* (PRE); Stellenbosch, Devon Valley Hotel at garden fence, on soil, (–DD), *S.M. Perold 1990* (PRE); Stellenbosch, Devon Valley Hotel, on soil bank behind hotel, (–DD), *S.M. Perold 1996* (PRE); Stellenbosch, (–DD), *T.R. Sim CH 1284* (PRE); S Paarl, Landskroon, in kloof, (–DD), *Volk 81/071* (BOL, PRE). 3319 (Worcester): W of Franschhoek, Waterval Farm, on earth bank, ditch next to dirt road, (–CC), *S.M. Perold 633* (PRE); 4 km N of Villiersdorp, Elandsriver Road, Du Toitsberge, near waterfall on Sneeukop, (–CD), *S.M. Perold 623* (PRE). 3322 (Oudtshoorn): George, NE of Hawthorndene Hotel, at roadside on side of earth water furrow, (–CD), *S.M. Perold 920* (PRE). 3418 (Simonstown): Constantia, on soil on damp rock face, (–AB), *S.M. Perold 656* (PRE).

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