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Studies in the Sphaerocarpales (Hepaticae) from southern Africa. 1. The genus *Monocarpus* and its only member, *M. sphaerocarpus*

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ABSTRACT

A taxonomic account of the genus *Monocarpus* and its only species, *M. sphaerocarpus*, is presented. The species was initially discovered on salt pans in Western Australia, and only later, in southern Africa. It is extremely rare and the structure of the minute thalli is difficult to determine, also to describe and to illustrate. As far as could be determined, no SEM micrographs of the thalli and spores have been published before, nor has the capsule wall been illustrated.

INTRODUCTION

In my recent treatment of the Marchantiidae (Part 1: Marchantiopsida) for the *Flora of southern Africa* (Perold 1999), I excluded the Sphaerocarpales (subclass Sphaerocarpidae), as very little new material had been collected since the last investigations of its constituent genera, namely *Monocarpus* by Schelpe (1969), *Riella* by Wigglesworth (1937), and *Riella* and *Sphaerocarpos* by Proskauer (1955). Fortunately, a few new local collections of *Sphaerocarpos* and *Riella*, have recently come to hand. It is also deemed essential to publish SEM micrographs of the thalli and particularly the spores of these taxa, which has, with rare exceptions, not been done before.

MATERIAL AND METHODS

A few thalli of the only southern African gathering (to date) of *Monocarpus sphaerocarpus*, *Toelken 1586a*, were carefully removed from the substrate and washed with water gently squirted from a pipette to remove the soil particles. Remaining particles were manually removed by using fine-tipped forceps. One thallus was vertically sectioned into two halves, which were mounted in water on a slide, to examine the air spaces in the outer, protective tissues. Two other thalli were carefully slit open to remove the carpocephala and in one, the capsule was also excised. The barrel air pores and cells in the carpocephalum wall, as well as the cells in the capsule wall and the spores (mounted in Hoyer's medium) were studied and photographed under a compound light microscope.

The remaining portion of the cleaned specimen was fixed in FAA (formaldehyde/alcohol/ glacial acetic acid and distilled water in proportion of 2:1:1:20); dehydrated in an ascending series of acetone to 100% and critical point dried in a Balzers Union dryer, using liquid CO_2 as the transitional fluid. The thalli (and air dried spores) were mounted on aluminium stubs with double-sided sellotape, gold-coated, then viewed and photographed, using an ISI SX 25 scanning electron microscope.

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This plant is most interesting, but unfortunately I have had to 'make do' with scanty, 30-year-old material and was loath to sacrifice any more thalli than were absolutely necessary for my investigations.

Specimens examined

WESTERN CAPE.—3320 (Montagu): near Montagu, roadside, 300 yds from Baths Hotel, saline depression under *Suaeda fruticosa* (with *Tortula splachnoides*), (–CC), 6-10-1968. *H. Toelken 1586a* (BOL, MEL).

AUSTRALIA.—Far north-west Victoria, red ochre pits at NW edge of the Raak plain; on damp saline mud amongst halophytic shrubs, 1 Aug. 1968. *J.H. Willis* (*MELI28508, BOL58350*).

TAXONOMIC HISTORY AND AFFINITIES

The generic name, *Monocarpus* was selected by Carr (1956) for this unique Australian liverwort. He thought it advisable to raise a new suborder for it, Monocarpineae. To quote him: 'The affinities of this suborder would be with the Sphaerocarpineae on the one hand and with the section Caudiciformes of Marchantiineae on the other'. Later the generic name was changed to *Carrpos* by Proskauer (1961a), on the grounds that Post & Kuntze (1903) had created an orthographic variant, *Monocarpus*, for *Monocarpia* Miquel (1865), a genus in the Annonaceae. Proskauer argued that, 'if one *Monocarpus* is an orthographic variant of *Monocarpia*, another is also, whether based on the same type or not'. Bullock (1961) soon pointed out, however, that *Monocarpia* Miq. and *Monocarpus* D.J.Carr are not homonyms; also, that the correction of *Monocarpia* Miq. by Post & Kuntze to '*Monocarpus*' was not permissible and that this did not make *Monocarpus* a new and superfluous name.

Proskauer (1961b) concluded that phylogenetically, *Carrpos* did not represent an intermediate between the Sphaerocarpales and the Marchantiales, but rather an offshoot from a 'pre-*Riccia*' pool, well within the Marchantiales. He referred it to his new family, Carrpaceae. Originally, Grolle (1972) had adopted *Carrpos* and accepted the family Carrpaceae. Later, Grolle (1983) agreed that, under the Sydney ICBN, Article 63.1 (Voss *et al.* 1983), *Monocarpus* Post & Kuntze was an invalid

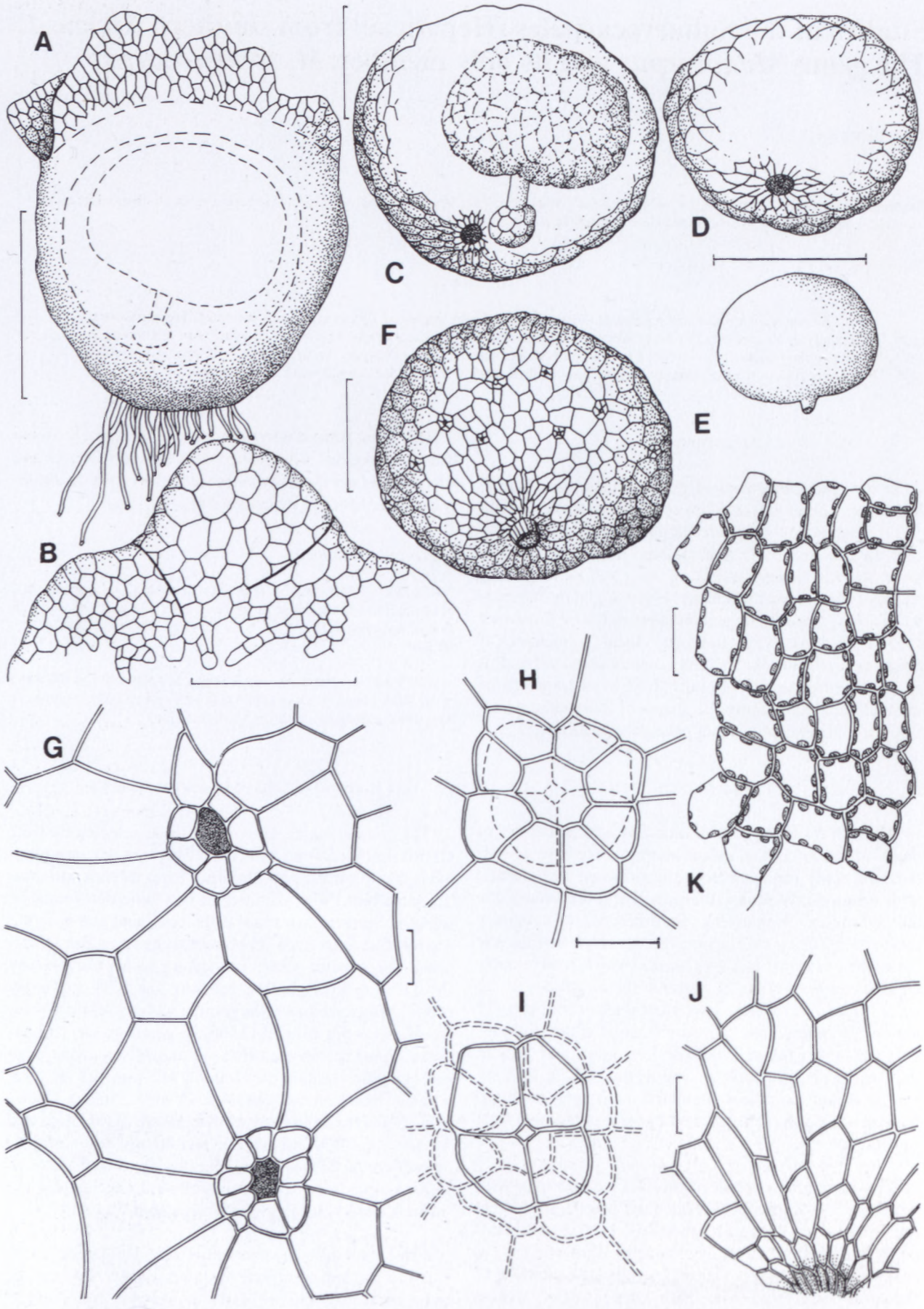

FIGURE 1.—*Monocarpus sphaerocarpus*. A, side view of thallus with bulging air chambers above and inside, capsule, seta and foot (stippled lines) enveloped by carpocephalum wall; B, above, domed air chambers separated by septa, below, cellular outgrowths from margin of pouch, arching over part of orifice; C, carpocephalum containing capsule with spores and below, short seta and bulbous foot; D, carpocephalum with capsule, seta and foot excised; E, excised capsule with part of seta; F, wall of carpocephalum with pores and part of stalk below; G, 2 air pores in wall of carpocephalum; H, pore from above; I, pore from below; J, cells in wall of carpocephalum decreasing in size toward stalk, the latter only partly shown; K, capsule wall with thickenings. A–K, *Toelken 1586a*. Scale bars: A, B, 1mm; C, F, 500 µm; D, E, 800 µm; G–J, 25 µm; K, 50 µm. Artist: G. Condy.

orthographic variant of the legitimate *Monocarpia* Miq. Hence, *Monocarpus* D.J.Carr was legitimate and *Carrpos* Prosk. was superfluous.

The generic name *Carrpos* continued, however, to be in use for some time to come. Schelpe (1969), in recording the only southern African find of this rare species [*Toelken 1586a* (BOL, MEL)], referred to it as *Carrpos sphaerocarpos* (D.J.Carr) Prosk. Because, according to Schelpe, Carr did not validate his proposed family, Monocarpaceae, Schelpe proceeded to do so, evidently unaware of Proskauer's Carrpaceae (Proskauer 1961b). He also thought that its taxonomic position appeared to be intermediate between the Sphaerocarpales and the Marchantiales, and he was 'disinclined to follow Carr in placing this family in the Marchantiales', preferring to 'wait for the discovery of male gametophytes'. He clearly did not know that Proskauer (1961b) had shown the species to be monoicous, with antheridia hidden in the air chambers of the thallus and difficult to find.

In Magill & Schelpe's (1979) checklist of the bryophytes of southern Africa, the species is also referred to as *Carrpos sphaerocarpos*, in the family Monocarpaceae D.J.Carr ex Schelpe. Schuster (1963) also considered *Carrpos*, as he called it, to belong to the Marchantiales and placed it in the monotypic suborder Carrpineae. In 1966, however, he incorporated it in the suborder Corsiniineae. Later on, Schuster (1984) again referred it to the suborder Carrpineae. Markham (1980) followed suit and referred to the species as *Carrpos sphaerocarpos*, stating that, on phytochemical evidence, *Carrpos* should be 'aligned near *Sphaerocarpos*, either in a separate suborder, or better, as Grolle (1972) had suggested, in a separate family'.

Grolle (1983) accepted Markham's 'strong biochemical evidence that a position in the Sphaerocarpales or close to the Sphaerocarpaceae may be more natural for this family than a placement in the Marchantiales as adopted by most authors following Carr'.

Scott (1985) followed Grolle, placing the Riellaceae, Sphaerocarpaceae and Monocarpaceae in the order Sphaerocarpales. In 1992 Schuster commented that this was done 'on surely erroneous bases'. In the present treatment, Grolle (1983) and Scott (1985) are followed.

Suborder **Monocarpineae**. Carr: 187 (1956).

Thalli terrestrial, ephemeral, reduced, pouch-like, medianly without an epidermis, open spaces formed above, separated by sloping or vertical septa; cells all thin-walled, oil bodies absent. Further growth sympodial by ventral sprouts, sometimes branched. *Ventral scales* and mucilage hairs lacking. *Rhizoids* all smooth, vertical.

Monoicous. *Antheridia* developed inside air chambers, stalk uniseriate, long, necrotic. *Archegonia* usually 3 per archegoniophore, but generally only 1 fertilised, neck with 6 canal cells. *Carpocephalum* closely surrounded by gametophytic tissue, its wall containing barrel pores opening into inner air chambers. *Capsule* with unistratose wall; cleistocarpous. *Seta* short, dark coloured, with bulbous foot. *Stalk* reduced, dark brown, lacking rhizoid furrow. *Spores* hemispherical, medium-sized, densely covered with fine tubercles, only released after dissolution of capsule wall and decay of surrounding gametophytic tissues. *Elaters* absent.

Monocarpaceae *D.J.Carr* in Australian Journal of Botany 4: 187 (1956).

Carrpaceae Prosk.: 375 (1961b).

The diagnoses of the monogeneric family and the monotypic genus are contained in the above description of the suborder Monocarpineae.

Monocarpus sphaerocarpus *D.J.Carr* in Australian Journal of Botany 4: 175 (1956). Type: Australia, northwestern Victoria, by the side of Calder Highway at Yatpool, adjacent to Red Cliffs, on bare mud of saltpan, August 1955, leg. *S.G.M. Carr* (née *Fawcett*) *s.n.* (MEL, holo.).

Carrpos sphaerocarpos (D.J.Carr) Prosk.: 155 (1961a).

Thalli ephemeral, gregarious, pouch-like, subspherical, somewhat flattened at poles, flanks slightly bulging, minute to small, 0.5–2.25 mm diam., up to 1.6 mm high (Figure 1A), mostly single-lobed, rarely double, pale green; outer, protective layers soon developing air spaces, at maturity closely surrounding carpocephalum (Figure 2A, B), which is usually single and subglobose,

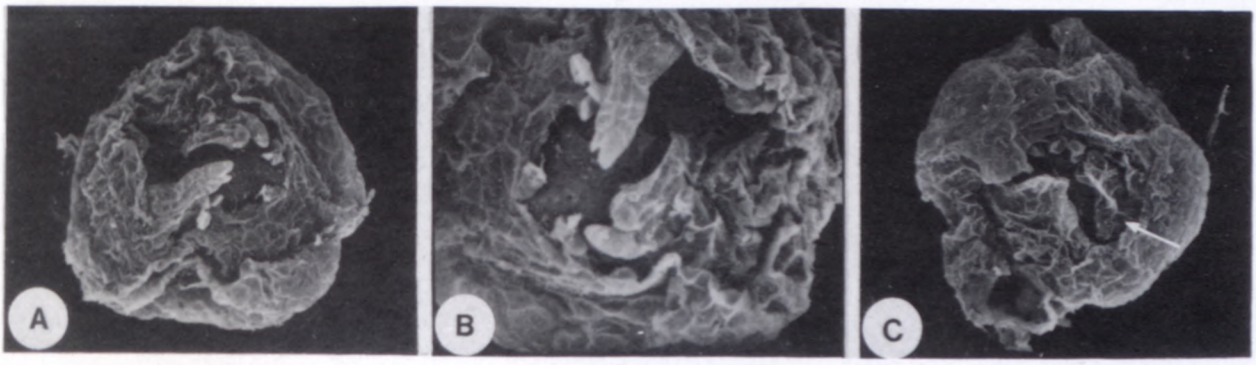

FIGURE 2.—*Monocarpus sphaerocarpus*. A, B, pouch-like thallus from above, outer protective layers closely surrounding carpocephalum, with cellular outgrowths from upper margin of pouch, arching over orifice at top; B, more enlarged; C, different thallus, showing unistratose septum (arrowed) and short, ventral sprout toward lower left corner. A–C, *Toelken 1586a*. A, × 34; B, × 53; C, × 35.

its uppermost wall remaining partly exposed, through which, brown colour of ripe spores and enclosing capsule wall visible; further growth of thallus by ventral sprouts (Figure 1C), which may be branched and have dorsally open air chambers; when dry, rather shrivelled, but otherwise not much altered, 'wings' of thallus regarded as being permanently in 'rolled up' state. *Pouch (or wing) tissue* at upper margin overarching and partly covering orifice over top of carpocephalum with cellular outgrowths (Figures 1B; 2A, B), sometimes even overlapping, terminal cells 30–40 × 25–30 µm, paler, but not glandular in appearance; cells in outer walls covering ± 2 rows of domed air chambers (Figure 1B), 4- or 5-sided, thin-walled, 40–75 × 22.5–50.0 µm, oil bodies absent, in fresh thalli containing many small chloroplasts, inner walls often bearing lamellae and complete or incomplete unistratose septa, these subdividing the air chambers, which are up to 450 µm high, 500 µm wide across base, into smaller ones, lacking photosynthetic filaments and opening toward inside through unspecialised openings into secondarily delimited cavities; before expansion of carpocephalum entire upper tissue consisting of elongated air spaces, apically open and separated by unistratose septa. *Basal part* of thallus fleshy, where supporting stalk of archegoniophore, without costa, scales and mucilage hairs absent; rhizoids produced only from underside of base of thallus, anchoring it to substrate, all vertical, smooth, lacking tubercles, colourless, 10–15 µm wide, not very numerous.

Monoicous. *Antheridia* with body ovoid, ± 80 µm wide, initially green, but white at maturity, pedicel uniseriate, disproportionately long and filamentous, turning brown and seemingly necrotic, arising from floor or lower part of walls of ordinary air chambers, mostly single per chamber, but difficult to find. *Archegonia* usually with 6 rows of neck cells and 4 lid cells, borne on archegoniophores. *Carpocephalum* (Figure 1C, D, F) with 1(2) receptacle(s), each with 1–3(–6) archegonia, but generally only one becoming fertilised, ± ovoid, up to 1475 × 1400 µm, wall hyaline, membranous, cells 5- or 6-sided, 70–125 × 55–105 µm, tapering slightly toward ends, in upper part interrupted by two-tiered barrel pores (Figure 1G), 75–150 µm apart, more or less evenly scattered; pores small, from above (Figure 1H) 6–8-sided, ± 15 × 20 µm, quite thick-walled, surrounded by a row of 6–8(9), radially arranged, small cells, 15–20 × 15–20 µm (occasionally some cells larger), often narrowing toward base, overlying inner, smaller pore (Figure 1I), ± square or rectangular, with surrounding 4 (or occasionally more) cells opening into narrow air chambers along inner wall of carpocephalum; chamber walls degenerate in older material and only strands of amorphous tissue with chloroplasts remaining; sometimes a thickened knot of heavily proliferated tissue observed in lateral wall of carpocephalum, here without air pores and air chambers, the cells almost rectangular and closely appressed, also reduced in size to 45–55 × 15–20 µm. *Stalk* short, up to 100 µm wide, 5 cell rows across, cells angular, 15–20 × 17.5–22.5 µm, walls dark brown, surrounding cells in carpocephalum wall (Figure 1J) reduced in size, 55–65 × 12.5–25.0 µm. *Capsule* at maturity practically filling space within carpocephalum, walls of both structures closely appressed; initially, however, its growth rate slower and young capsule only occupying part of space within (Figure 1C); capsule wall (Figure 1K) unistratose, brown, composed of thin, ± rectangular to somewhat irregularly shaped cells, 25–50 × 30.0–57.5 µm, along walls 2–4 small nodular to elongated thickenings, quite often joined into a continuous, uneven line, cells separating easily. *Seta* dark brown, only ± 100 × 50 µm, composed of central row of cells and marginally surrounded by 5 or 6 cells in tiers. *Foot* bulbous, ± 120 µm long, up to 100 µm wide, consisting of a cluster of cells. *Spores* at maturity, seemingly regardless of size of capsule, 42.5– 50.0 µm diam., dark brown, light brown spores presumably younger, 27.5–35.0 µm diam., hemispherical; distal face (Figure 3A–D) convex, densely covered with numerous fine tubercles, ± 2.5 µm long, in 18 or 19 rows across, some central ones crowned with a small papilla, others smooth, joined by low walls which enclose tiny, shallow pits; around spore periphery, many fine, projecting tubercles; proximal face (Figure 3E) without triradiate mark, slightly indented, central part also covered with fine tubercles separated by tiny pits, broad rim around margin (Figure 3E, F) without ornamentation, but not quite smooth; spore release occurring on dissolution of capsule wall and by decay of carpocephalum wall as well as surrounding thallus tissue. *Elaters* absent.

Distribution

In spite of a detailed map, kindly drawn and sent by Dr H. Toelken, now of the State Herbarium, Adelaide, Australia, and also my own repeated visits to the Baths Hotel grounds near Montagu in Western Cape (Figure 4), I have not succeeded in finding more material of this minute plant. My failure may perhaps be attributed to considerable building operations in the vicinity in recent years, possibly leading to the complete disappearance of the species from this locality.

Ecology

The plants grew on saline-gypsum soil in the winter rainfall region of Western Cape and appear to be extremely rare. According to Low & Rebelo (1996) the vegetation type in this locality is Central Mountain Renosterveld of the Fynbos Biome, sclerophyllous, microphyllous vascular plant vegetation (Cowling *et al.* 1997; Rutherford 1997). In Australia, mainly in NW Victoria, Scott (1985) reported them to be growing on salt-rich and gypsum-rich soils at salt pans, where the ground rises out of the saline influence but is kept moist.

DISCUSSION

Proskauer (1961b) complained of *Monocarpus sphaerocarpus* that, 'the material is difficult to handle. Not only are the cells delicate and readily damaged, but even the larger thalli (which in reality are still minute), have most awkward shapes'. I would readily agree with this observation. Proskauer also found that 'even the best special photographic lenses at the required magnifications lack the requisite depth of focus'. Fortunately, the SEM overcomes such problems, but, regrettably, I had no fresh material to study. Proskauer further commented that, 'the thallus proved to be rather more complex than described (by Carr), a discrepancy explained by the type field material having been both somewhat depauperate

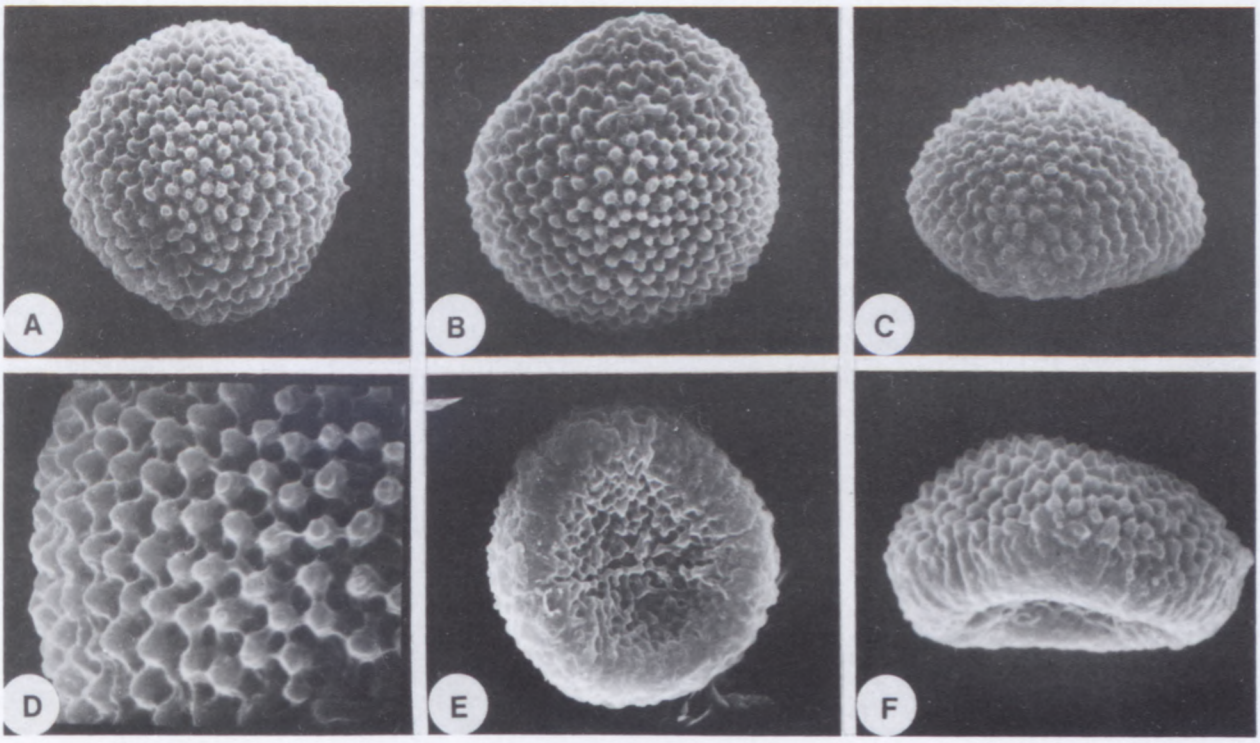

FIGURE 3.—*Monocarpus sphaerocarpus*. Spores. A, B, distal face; C, side view of distal face; D, detail of margin of distal face; E, proximal face; F, side view. A–F, *Toelken 1586a*. A, × 805; B, × 909; C, × 933; D, × 2312; E, × 852; F, × 1017.

and precociously fertile, with the expanding archegoniophore compressing the vegetative tissues'. Poor environmental conditions and harvesting prior to maturation of the spores were held responsible for this (Proskauer 1961b). To these observations I would like to add that the South African field-grown thalli (although considerably smaller), are more easily matched with Carr's descriptions and illustrations than with the elongated, richly sprouting and branched thalli, cultivated on various media under artificial conditions (on a window sill), that were illustrated and described by Proskauer. He found, significantly, that different media influenced the size of the plants. Scott's (1985) photograph of *Monocarpus sphaerocarpus* also shows rounded, pouch-like thalli, sometimes 2-lobed, but lacking elongated ventral sprouts.

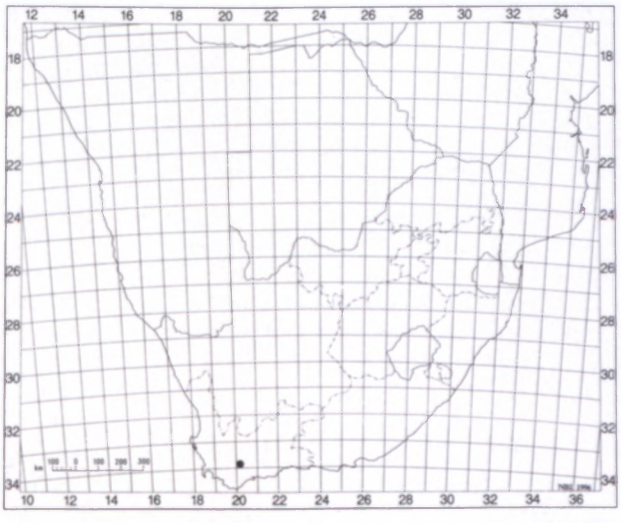

FIGURE 4.—Distribution of *Monocarpus sphaerocarpus* in southern Africa.

Carr (1956) described the barrel pores of the 'involucre' (= carpocephalum) as frequently having 6–8 epidermal cells and only 4 hypodermal cells, with a much larger, generally octagonal or hexagonal outer pore and a small, roughly square or rectangular inner pore. In unfertilised material that he examined, Proskauer on the other hand, generally found only 4 cells in each of the outer and inner rings of cells, although not uncommonly, there were also pores with up to 8 cells in the outer, as well as in the inner ring; a few pores, apparently, showed a considerably wider external than internal opening. My findings on the pores match those of Carr more closely.

A suture representing the closure of the mouth of the 'involucre', where the cells were clavate and much larger than the other 'involucral' cells, was described by Carr (1956). According to Proskauer, the occlusion of the receptacle, described by Carr as 'a routine post-fertilisation change, did not take place'. I cannot comment on this, not being able to study living material at different stages of development. It is possible that the 'thickened knot of heavily proliferated tissue' I observed in the carpocephalum wall, may represent the closure of the mouth, but this needs to be verified.

Carr referred to meiosis not being simultaneous throughout the sporogenous tissue, whereas Proskauer strongly doubted that meiosis in a sporophyte was other than simultaneous, but could not prove this, because he lacked suitable material. Proskauer, furthermore, suspected that Carr's sporelings seemed to have resulted from leptosporangiate fern spores. In the smallish to medium-sized capsules that I examined, no 'sterile cells' (Carr 1956; Proskauer 1961b) were observed. Carr, indeed, remarked that 'they may be entirely absent from very large capsules'.

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