# Studies in the Sphaerocarpales (Hepaticae) from southern Africa. 2. The genus *Sphaerocarpos* and its only local species, *S. stipitatus*

# S.M. PEROLD\*

Keywords: Austrosphaerocarpos (subgenus), Hepaticae, Monocarpineae, Riellineae, southern Africa, Sphaerocarpaceae, Sphaerocarpales, Sphaerocarpos stipitatus

#### ABSTRACT

A taxonomic account of the genus Sphaerocarpos, subgenus Austrosphaerocarpos, and its only local species, S. stipitatus Bisch. ex Lindenb., is presented here. These taxa are classified in the suborder Sphaerocarpineae of the order Sphaerocarpales, for which short notes and a key to all three constituent suborders, Monocarpineae, Riellineae and Sphaerocarpineae, are provided.

#### INTRODUCTION

The genus *Sphaerocarpos* (Micheli) Boehmer was first recorded from southern Africa by Proskauer (1954). He received material from the algologist, Dr M.A. Pocock, who had collected it in the Eastern Cape, on the banks of pools in the Palmiet River, a tributary of the New Years River, seven miles from Grahamstown, on the Cradock Road. Miss Lilian Britten, a lecturer at Rhodes University College, had originally discovered *Sphaerocarpos* plants at this locality. A further collection from Clanwilliam, by Prof. E.A.C.L.E. Schelpe, was also recorded by Proskauer.

Arnell (1963) did not report any new collections and the only recent published South African record of the species is by Long (1993) from a 1969 collection, *H.R. Toelken* 1978 (BM, BOL) from Paardeneiland, Cape Town.

Seven of the collections that I studied, have not been reported in the literature before. Despite repeated visits to the Northern, Western and Eastern Cape by various collectors, myself included, such a small number of gatherings must surely reflect the rarity of these plants, although Proskauer (1955) remarked that, 'one does not normally find members of the group in the field without being familiar with them'. Their truncated life cycle, from spore to spore, can take less than 45 days (Schuster 1992), and dramatically reduces the time period during which they are likely to be found.

It is, nonetheless, hoped that the present, fully illustrated paper, will familiarise more botanists with these remarkable plants and that, in future, they will collect them, thus enabling us to establish the local distribution range more completely. Previously, it was thought that *S. stipitatus* was restricted to the southern hemisphere, i.e. Chile in South America (where the type specimen had been collected by Bertero in 1829) and South Africa. Recently, however, it was also collected as a presumed adventive in Portugal (Sérgio & Sim-Sim 1989), as well as at a remote, high altitude locality in East Nepal (Long 1993), where its accidental introduction is unlikely. This paper on *Sphaerocarpos stipitatus*, is the second in a series of three on the Sphaerocarpales in southern Africa.

#### MATERIAL AND METHODS

The same procedures as outlined in Perold (1999b) were employed in the preparation of the material for examination and photography by compound light microscope and scanning electron microscope.

Order Sphaerocarpales *Cavers* in New Phytologist 9: 81 (1910); Grolle: 55 (1983); Scott: 63 (1985).

[excluding the American *Geothallus* Campbell and the Mesozoic fossil, *Naiadita* Brodie]

Plants ephemeral, very diverse, terrestrial; sometimes minute, subspherical and pouch-like, occasionally with branched ventral sprouts (Monocarpineae), or somewhat larger, with prostrate, median stems, up to 4 (or more) cell layers thick, pseudodichotomously branching, with wings 2-ranked, lateral, incised, leafy, unistratose (Sphaerocarpineae); otherwise aquatic, semifrondose, stems  $\pm$  erect, apical dominance seemingly persistent, with broad, undulating wing on dorsal side, small leaf scales at both sides and ventrally (Riellineae). Air chambers and air pores (the latter in the carpocephalum wall) present only in Monocarpineae. Cells all thin-walled, large, delicate; smaller oil cells found only in Riellineae. Rhizoids all smooth.

Asexual reproduction by gemmae, only in Riellineae.

Monoicous in Monocarpineae and rarely in *Riella* species, otherwise dioicous, mostly heterothallic, with male plants much or somewhat smaller. *Antheridia* ovoid to globose, in Monocarpineae located inside air chambers, pedicel long, uniseriate; in Sphaerocarpineae individually surrounded by involuces, crowded together on dorsal surface of stems; in Riellineae enclosed in pockets along margin of undulating wing, pedicel short, uniseriate. *Archegonia* with 6 rows of neck cells, in Monocarpineae borne on archegoniophores, otherwise individually surrounded by large, flask-shaped or pyriform involuces, dorsally on, or along stems of female plants. *Stalk* variable in length, without rhi-

<sup>\*</sup> National Botanical Institute, Private Bag X101, 0001 Pretoria. MS. received: 1999-07-02.

zoid furrow. *Capsule* globose, cleistocarpous, wall unistratose, cell walls delicate, in Monocarpineae only with small, nodular to elongated thickenings, in other suborders thickenings absent. *Seta* very short, becoming necrotic. *Spores* medium-sized to very large, 40–140 µm diam., single in Monocarpineae and Riellineae, mostly remaining in tetrads in Sphaerocarpineae. *Elaters* absent. *Nutritive cells* present in Sphaerocarpineae and Riellineae. Spore release in all three suborders by dissolution or decay of capsule wall and surrounding tissue.

#### Key to local suborders of Sphaerocarpales

1a Plants terrestrial; distribution confined to winter rainfall regions of southern Africa; highly diverse in appearance—subspherical and pouch-like or dorsiventrally flattened with lateral, leaf-like lobes; cells uniform, all lacking oil bodies; spores single or in tetrads:

dimorphic, some with an oil body; spores single, ornamentation various ...... suborder Riellineae R.M.Schust.

# Sphaerocarpineae Cavers. R.M.Schust.: 807 (1992).

Plants terrestrial, dorsiventrally flattened, bilateral, consisting of a stem (or axis), once or twice to repeatedly furcate, laterally invested with delicate, leaf-like lobes. *Ventral* scales absent, instead invested with ephemeral slime papillae. *Cells* thin-walled, lacking oil bodies. *Rhizoids* all smooth, hyaline.

#### Asexual reproduction absent.

Dioicous, heterothallic, male gametophytes much smaller than female ones. Antheridia individually developed inside small, unistratose, brownish purple, flasklike involucres, in acropetal sequence, crowded along stem dorsally. Archegonia also enclosed, almost always individually, in much larger, green, flask-like involucres, wall double-layered only in single South African species, S. stipitatus; in other species unistratose. Calyptra delicate, unistratose around cleistocarpous capsule, 3- or 4-stratose around short, necrotic seta and subspherical foot, disintegrating when spores reach maturity, allowing their release, when flask wall also decays. Spores in permanent tetrads in South African species, large, external face covered with ridges; in some extra-South African species separating at maturity, the spore ornamentation areolate to lamellate. Nutritive cells present, but elaters absent.

Sphaerocarpaceae (Dumort.) Heeg in Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien 41: 573 (1891) ('Sphaerocarpeae'); Müll.Frib.: 310 (1951–1958); S.W.Arnell: 8 (1963); R.M.Schust.: 810 (1992).

Tribe Sphaerocarpeae Dumort. 13: 163 (1874).

Subfamily Sphaerocarpoideae Schiffn.: 50 (1893); Engl.: 49 (1898).

The Sphaerocarpineae include only the single family, Sphaerocarpaceae; hence, the details in the subordinal description are not repeated here. Sphaerocarpos (Micheli) Boehmer in C.G. Ludwig, Definitiones generum plantarum: 501 (1760); Haynes: 219 (1910); Prosk.: 153 (1954); S.W.Arnell: 8 (1963); R.M.Schust.: 816 (1992). Type: S. michelii Bellardi.

Sphaerocarpos Micheli: 4, t. 3 (1729).

Sphaerocarpus Adanson: 15 (1763) [orth. var.]; Steph.: 655 (1899); Müll.Frib.: 310 (1951–1958).

Plants ephemeral, gregarious to scattered; stems once or twice (or more frequently) furcately branching, dorsiventrally flattened, laterally invested with delicate, succubously inserted, leaf-like lobes; ventrally (and apically) with scattered slime papillae; ventrally with smooth, hyaline rhizoids.

Dioicous, strongly heterothallic; gametangia individually enveloped by flask-shaped involucres, small in male plants, but much larger in females, which are sessile or stipitate, wall unistratose, only exceptionally bistratose, eventually containing globose capsule and short seta with foot. Spores remaining in tetrads or separating at maturity, ornamentation reticulate or ridged.

Species in the genus fall into two, well-defined groups that were recently segregated by Schuster (1992).

### Key to subgenera of Sphaerocarpos

Proskauer (1954) concluded that the specific epithet *stipitatus* for this species was apt, since such a stalk did not exist in any other species of the genus. The longest stalk that he measured was  $\pm 1.5$  mm. Recently, however, Long (1993) reported that in the material from Nepal and Portugal (Sérgio & Sim-Sim 1989), 'the female

flasks have an extremely short basal stalk'. The stalks I measured were also short, only 200–795  $\mu$ m in length, which would support Long's observation that, 'development of the stipe must be considered variable', hence the minor alteration I made to Schuster's (1992) key to the subgenus *Austrosphaerocarpus*.

Sphaerocarpos stipitatus Bisch. ex Lindenb., Verhandlungen der kaiserlichen Leopoldinisch-carolinischen deutschen Akademie der Naturforscher 10 (= Nova acta Academiae Caesareae Leopoldino Carolinae germanicae naturae curiosorum 18): 504 i (1837); Haynes: 228 (1910); Prosk.: 144 (1954); Prosk.: 63 (1955); S.W.Arnell: 8 (1963); Sérgio & Sim-Sim: 414 (1989); Long: 77 (1993). Type: Chile, Quillota, Bertero 695 (PC, holo.).

Sphaerocarpus berteri Mont.: 39 (1838); Nees: 369 (1838); Mont.: 50 (1839); Gottsche et al.: 595 (1846).

Sphaerocarpus berteroi Mont. orth. mut.; Steph.: 657 (1899); nom. inval., orthographic variant for S. berteri.

Plants ephemeral to short-lived, gregarious or scattered; stems once or twice, to repeatedly furcately branching and forming partial rosettes; markedly heterothallic, male gametophytes tiny (Figure 1A, B), antheridial flasks purplish brown, intimately associated with much larger ( $\times$  10), light green, female gametophytes. Stems somewhat indeterminate, in both sexes prostrate, dorsiventrally flattened, in the middle up to 260-300 µm thick, consisting of (2-)3 or 4 layers of thin-walled, 4- or 5-sided, elongated cells, 112.5-160.0 × 45-75 µm, ventral cell layer with scattered slime papillae,  $37.5-62.5 \times 17.5-22.5 \mu m$ , raised on smaller or larger basal cell; above mostly obscured by crowded gametangia, each with a small or large (depending on sex) flask-shaped involucre, produced in acropetal sequence, usually in 2 series; laterally giving rise to delicate, unistratose, translucent, alternate, succubously oriented, leaf-like lobes; ventrally anchored to substrate by rhizoids, all smooth, hyaline, 30-50 µm wide.

Dioicous. Male plants with branches (Figure 3A)  $1250-1750 \times 525-625 \ \mu m$ , tapering apically, close together and almost parallel to widely divergent, laterally with mostly obscured, leaf-like lobes (Figure 1C, D), fan-shaped, 650-1025 µm long, above 400-975(-1100) µm wide, narrowing toward base, 100-650 µm wide; upper marginal cells mostly subquadrate,  $40-50 \times$ 47.5-70.0 µm, middle laminal cells long-rectangular,  $132.5-145.0 \times 42.5-62.5 \ \mu\text{m}$ , basal cells  $125.0-137.5 \times 10^{-1}$ 75.0-87.5 µm. Antheridial involucres (Figures 2B; 3B, C) generally in 2 or 3 series along segments, sessile, flask-shaped, 250-280 µm high, apically contracted, opening surrounded by 7 or 8 vertically oriented cells,  $45.0-62.5(-92.5) \times 25-30 \ \mu m$ , their apices projecting somewhat, median sector inflated, width across 180-200 µm, wall unistratose, cells generally 4-sided, sometimes their walls bulging, mostly 50.0–67.5  $\times$  27.5–45.0  $\mu$ m. Antheridia (Figure 2A) individually nearly completely enclosed by flasks, only apical ones not discharged, ovoid,  $\pm 125 \times 82.5 \,\mu\text{m}$ , raised on short pedicel, up to  $57.5 \times 17.5 \ \mu\text{m}$ , consisting of uniseriate column of 5 cells.

Female plants pseudodichotomously branching 1-3 times, forming partial rosettes, 4.5-6.5 mm across, sometimes segments simple (Figure 1E) or nearly so,  $\pm$  $4.4 \times 2.6$  mm, lateral leaf-like lobes (Figure 1F-M) mostly single, occasionally bilobed, obovate, size variable,  $1075-2500 \times 625-3375 \,\mu\text{m}$  above, narrower below, 275-1125 µm wide; cells at upper margin (Figure 1N) usually isodiametric,  $55.0-57.5 \times 50.0-62.5 \mu m$ , thinwalled, sometimes cell projecting at angle much larger, ±  $52.5 \times 145 \ \mu\text{m}$ , cells at lateral margin  $87.5-125.0 \ \times$ 30.0-42.5 µm; upper laminal and median cells longhexagonal, 92.5-200.0  $\times$  50-70  $\mu$ m, basal cells 155.0-177.5 × 55-105 µm. Archegonial involucres often crowded together, obscuring leaf-like lobes (Figure 3D), sessile when first initiated, later stalked (Figure 3E), ellipsoidal or bluntly conical (Figure 2C-E), at maturity 1800-3000 µm high, width 750-1125 µm across widest, basal part, narrowing gradually upwards to mouth and generally more abruptly below towards stalk, mouth (Figure 3F) usually 250-300 µm wide, surrounded by unistratose ring of 16 or more hyaline cells,  $100-105 \times$ 50-60 µm, rounded above and projecting somewhat crenulately; rarely, larger involucre containing 2 sporophytes (Figure 2F), 3625  $\mu$ m high, at mouth ± 625  $\mu$ m wide, 2050 µm wide across basal part; below mouth rest of involucral wall double-layered: outer cells hyaline, chloroplasts absent, long-rectangular above (Figure 2I), 125.0–147.5  $\times$  40.0–42.5  $\mu m,$  lower down gradually enlarging (Figure 2H), 5- or 6-sided, 150-300 × 75-125 µm; inner cells (Figure 2J-L) finger-like, much more numerous, in clusters, rich in chloroplasts, with free, downward curving, papilliform tips, up to  $185 \times 32.5 \,\mu m$ in upper part of flask, smaller lower down and often becoming partially destroyed. Stalk developing by intercalary growth, length variable, 200-795 µm, width 175-250 µm, in cross section (Figure 2G) mostly with 6 cells across, cells in outer row  $30-40 \times 40-60 \ \mu\text{m}$ , inner cells in 4 rows,  $\pm$  75  $\times$  75  $\mu$ m. Calyptra remaining unruptured for a long period enveloping mature capsule, seta and foot (Figure 2M) hyaline, mostly unistratose, cells 4–6-sided, 65–145  $\times$  65–100  $\mu$ m, smaller above, where crowned by persistent archegonial neck (Figure 2N) and below, where closely investing seta and foot, here up to 4-stratose. Archegonial neck 75-85 × 30.0-37.5 µm, formed by 6 rows of cells and reportedly (Schuster 1992) with only 2 neck-canal cells. Capsule 650-825 µm diam., wall (Figure 2Q) unistratose, lacking thickenings, cells  $\pm$  5-sided, 37.5-65.0  $\times$  37.5-50.0  $\mu$ m, densely covered with starch granules, particularly when young; with age their number apparently reduced, subround or oval,  $5.0-12.5 \times 5-10 \ \mu\text{m}$ . Seta (Figure 2O) with 4 cell rows, very short,  $\pm 100 \times 40 \,\mu\text{m}$ , becoming necrotic. Foot partly fused with calyptra below, bulbous,  $\pm 270 \times 220 \,\mu\text{m}$ , resting on 'platform' of cells filling basal part of flask, cells  $100-170 \times 75-125 \,\mu\text{m}$ ; in cross section (Figure 2P) centrally with several 'haustorial' cells, roughly triangular, corners rounded,  $\pm 42.5 \,\mu m$  long, up to 47.5  $\mu m$  wide across widest part, surrounded by thin layer of non-cellular tissue and then by 2 or 3 rows of hyaline cells, the largest, outermost cells  $30.0-37.5 \times 32.5-37.5 \ \mu m$ . Spores remaining in tetrads, 87.5-112.5 µm diam., yellow-brown to dark brown; 3 (Figure 4C) or all 4 spores (Figure 4A, B, D, E) of tetrad visible at the same time, joined at thin line in narrow groove (Figure 4F),  $\pm 2.5$  $\mu$ m wide, ornamentation ridged, with 16–19 minutely

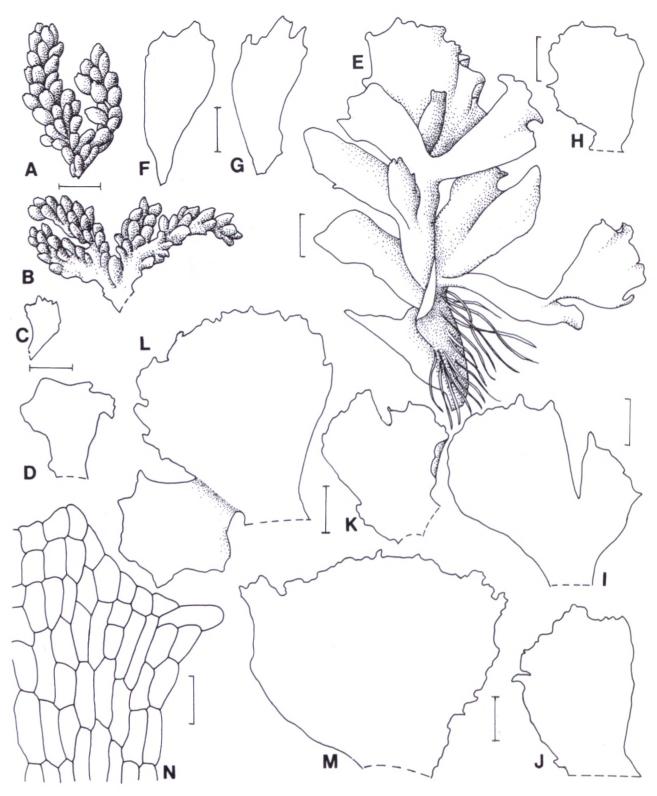


FIGURE 1.—Sphaerocarpos stipitatus. A, B, dorsal view of male gametophytes with antheridial involucres; C, D, young male, and older, leaf-like lobes, respectively; E, dorsal view of female gametophyte with stem ('axis') and lateral, leaf-like lobes; F–M, female leaf-like lobes; N, detail of leaf-like lobe. A–N, Koekemoer 1425. Scale bars: A–M, 500 µm; N, 100 µm. Artist: Gillian Condy.

papillate ridges, sometimes branched and up to 10  $\mu$ m apart, running from centre of distal faces outward and stopping short at groove, rarely forming incomplete areolae. *Nutritive cells* (Figure 2R1-3) generally ovoid, 42.5-50.0 × 30.0-37.5  $\mu$ m, apparently with several nuclei (4-8), resulting from mitoses and therefore remaining diploid, sometimes 4-celled; although containing starch granules and chloroplasts, their role in nutrition of developing spores not proven. Release of spores and nutritive cells by disintegration of the capsule wall, then by the calyptra and finally by the wall of the flask.

#### DISCUSSION

The genus *Sphaerocarpos* has aroused much interest, because sex chromosomes in plants were first found in *S. donnellii* by Allen (1919). Since then, it has been

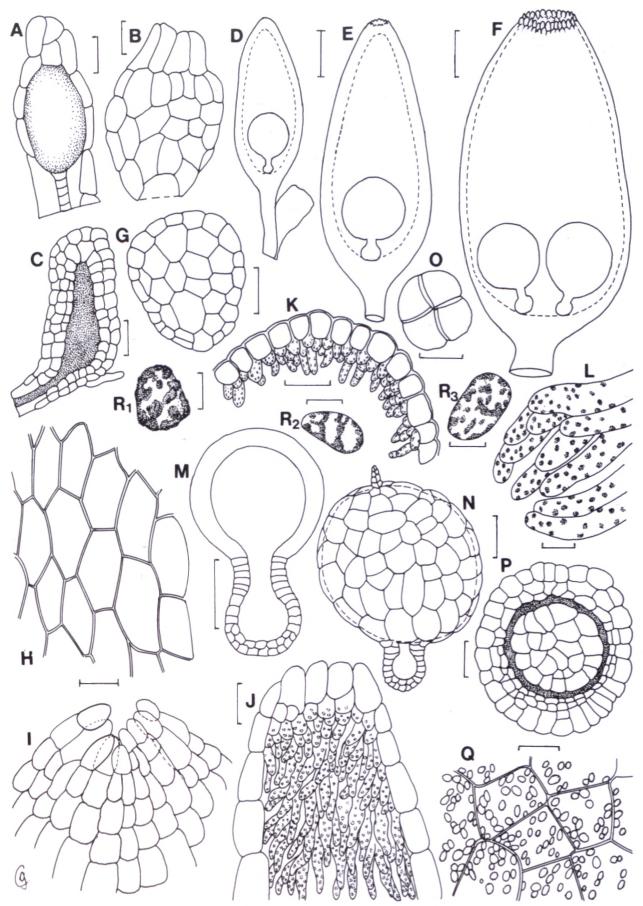


FIGURE 2.—Sphaerocarpos stipitatus. A, male involucre containing antheridium partly exposed; B, male involucre; C, archegonium and flask; D, E, older flasks; F, large flask with 2 capsules; G, c/s stalk; H, cells in outer wall of flask (without chloroplasts). I–L, wall of flask: I, mouth and upper part from outside; J, mouth and upper part with papilliform cells from inside; K, c/s with larger, clear outer cells and smaller, inner cells containing numerous chloroplasts; L, inner cells more enlarged. M, younger capsule, with seta and foot enveloped by calyptra; N, calyptra, above with persistent archegonial neck, below covering seta and foot; O, c/s seta; P, c/s foot; Q, capsule wall without thickenings, but covered with starch grains; R<sub>1</sub>–R<sub>3</sub>, nutritive cells. A–R<sub>3</sub>, *Koekemoer 1425*. Scale bars: A–C, L, P, 50 μm; D–F, 500 μm; G–K, 100 μm; M, N, 200 μm; O, Q, R<sub>1</sub>–R<sub>3</sub>, 25 μm. Artist: Gillian Condy.

21

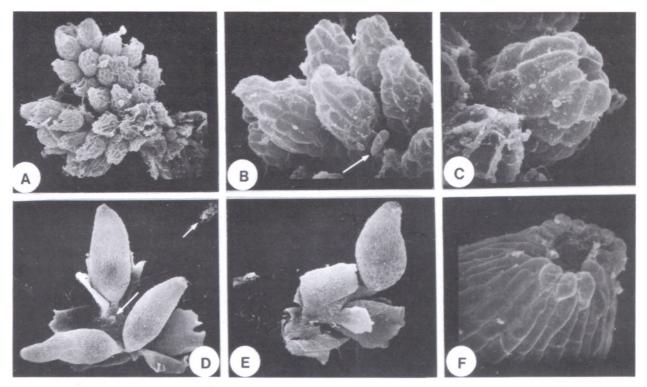


FIGURE 3.—Sphaerocarpos stipitatus. A, male plant covered with numerous antheridial involucres; B, antheridial flasks, with arrow indicating upper cell of slime papilla; C, mouth of antheridial flask; D, female plant with leaf-like lobes and 3 flasks, 4th flask removed, remainder of its stalk indicated by arrow; at top, right corner tip of male branch covered in flasks, to compare difference in sizes of male and female plants; E, female plant with single flask on longer stalk, partly hidden by leaf-like lobe; F, mouth of female flask. A–F, Koekemoer 1425. A, × 45; B, × 135; C, × 254; D, × 8.5; E, × 14; F, × 83.

repeatedly studied with regard to its genetics and cytology; furthermore, a number of cultures have been maintained for lengthy periods of time.

In several aspects, the gametophyte, with its prostrate stem (or axis) and delicate, 2-ranked, succubously inserted leaf-like lobes, resembles *Fossombronia* species, but so-called 'angle' leaves at the fork of dichotomies, as described by Proskauer (1954) and Schuster (1992), have not been observed by me in the present study, although I. am familiar with them from my work on the Fossombroniaceae (Perold 1999a).

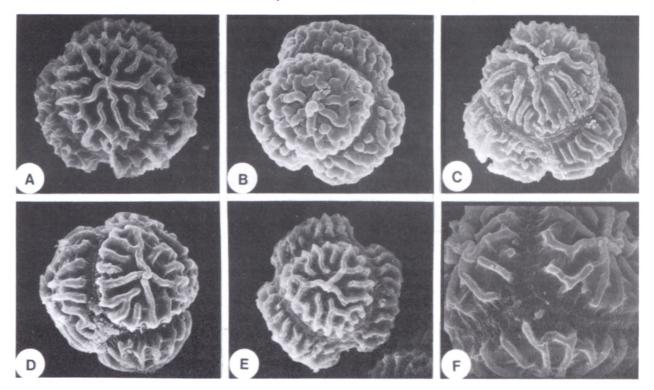


FIGURE 4.—Sphaerocarpos stipitatus. A–E, spore tetrads; F, groove where 3 of tetrads are joined. A, E.A.C.L.E. Schelpe 4877 (BOL); B, Toelken 1978 (BOL); C, A.S.L. Schelpe 760 (BOL); D, S.M. Perold 1838; E, Koekemoer 1425; F, Oliver 8961. A, D, × 366; B, × 439; C, × 374; E, × 347; F, × 682.

The gametophyte in *Sphaerocarpos* species is delicate and lacks physiological drought resistance (Schuster 1992); it is, nevertheless, adapted to warm and sometimes disturbed areas, with adequate moisture only seasonally and with intervening long, dry periods. It is regarded as an ecological specialist and is a temporary component of vegetation that frequently endures drought in summer. To cope with such an environment, its life cycle is considerably shortened and development of the sporophyte is accelerated; it survives the dry periods as spores, which generally remain in tetrads, eventually giving rise to two male plants in close proximity to two female plants, thus ensuring that fertilisation takes place and that a new generation will ensue.

In using a molecular approach by determining sequences for the 18S-r RNA gene to construct phylogenetic trees of a number of bryophytes, Capesius & Bopp (1997) concluded that the Sphaerocarpales diverged early as a separate clade among the Marchantiopsida.

## Ecology

In southern Africa, S. stipitatus is restricted to the winter rainfall regions of the Northern, Western and Eastern Cape, which experience hot, dry summers (Figure 5). The plants grow at altitudes ranging from sea level to  $\pm 1\,200$  m, on moist, fine-grained, sandy to clayey soils or on mud; at drainage ditches, water courses or on earth banks; under fynbos, short karroid scrub or grass, often together with mosses and *Riccia* species. The localities fall in several different vegetation types, namely Mountain Fynbos, Upland and Lowland Succulent Karoo, as well as Grassy Fynbos (Low & Rebelo 1996). Dates when sporulating material was collected, range from the end of July to early October.

Specimens examined

Britten 58348 (BOL).

Koekemoer 1425 (PRE).

Magill & Schelpe 3961A (PRE).

Oliver 8961 (PRE).

Perold 1838 (PRE).

A.S.L. Schelpe 760 (BOL58344); E.A.C.L.E. Schelpe 4877 (BOL58346), 4918b (BOL58345).

*Toelken 1978* (BM) (*BOL58347*) (ridges rather thicker in the spores from this specimen; see Figure 4B).

#### ACKNOWLEDGEMENTS

My sincere thanks are extended to Dr D.G. Long for kindly refereeing this paper, to the Curator of BOL for the loan of specimens; to Dr O.A. Leistner for his valuable advice and to my colleagues at NBI for kindly collecting specimens of *S. stipitatus*, and particularly, to Ms M. Koekemoer, Curator of PRE, for collecting and carefully tending live material; also to Ms G. Condy for the drawings; Mrs A. Romanowski for developing and printing the micrographs and to Ms D. Maree for typing the manuscript.

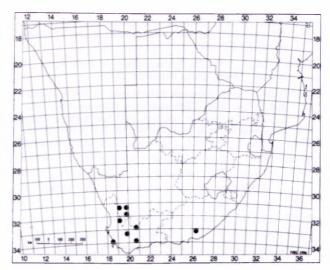


FIGURE 5.—Distribution of *Sphaerocarpos stipitatus* in southern Africa. Pocock specimen not indicated on map (grid reference 3326AD), because I did not examine it.

#### REFERENCES

ADANSON, M. 1763. Famille des Plantes 2: 1-640. Vincent, Paris.

- ALLEN, C.E. 1919. The basis of sex inheritance in Sphaerocarpos. Proceedings of the American Philosophical Society 58: 289-316.
- ARNELL, S.W. 1963. *Hepaticae of South Africa*. Swedish Natural Science Council, Stockholm.
- CAPESIUS, I. & BOPP, M. 1997. New classification of liverworts based on molecular and morphological data. *Plant Systematics* and Evolution 207: 87–97.
- CAVERS, F. 1910. The inter-relationships of the Bryophyta. New Phytologist 9: 81-91.
- DUMORTIER, B.C.J. 1874. Hepaticae Europae. Bulletin de la Société Royale de Botanique de Belgique 13: 1–203.
- ENGLER, A. 1898. Syllabus der Pflanzenfamilien, edn 2: 49.
- GOTTSCHE, C.M., LINDENBERG, J.B.G. & NEES AB ESEN-BECK, C.G. 1846. Synopsis hepaticarum. Meissner, Hamburg. Reprinted 1967, Cramer, Lehre.
- GROLLE, R. 1983. Nomina generica hepaticarum: references, types and synonymies. Acta Botanica Fennica 121: 1–62.
- HAYNES, C.C. 1910. Sphaerocarpos hians sp. nov., with a revision of the genus and illustrations of the species. Bulletin of the Torrey Botanical Club 37: 215-230.
- HEEG, M. 1891. Verhandlungen der kaiserlich-königlichen zoologischbotanischen Gesellschaft in Wien 41: 573 ('Sphaerocarpeae').
- LINDENBERG, J.B.W. 1837. Nachträge zur Monographie der Riccieen. Verhandlungen der kaiserlichen Leopoldinisch-carolinischen deutschen Akademie der Naturforscher 10 (= Nova acta Academiae Caesareae Leopoldino Carolinae germanicae naturae curiosorum 18): 504. i. t. 32.
- LONG, D.G. 1993. Notes on Himalayan Hepaticae 1. Sphaerocarpos subg. Austrosphaerocarpos Schust. in the Nepal Himalaya. Journal of the Hattori Botanical Laboratory 74: 77-81.
- LOW, A.B. & REBELO, A.G. (eds). 1996. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs & Tourism, Pretoria.
- LUDWIG, C.G. 1760. Definitiones generum plantarum. Leipzig.
- MICHELI, P.A. 1729. Nova plantarum genera. Firenze.
- MONTAGNE, J.F.C. 1838. Centurie des plantes cellulaires exotiques nouvelles. Annales des Sciences Naturelles, Bot. Sér. 2, 9: 38-57
- MONTAGNE, J.F.C. 1839. Florula boliviensis. In A. d'Orbigny, Voyage dans l'Amérique méridionale 7, part 2. Paris.
- MÜLLER, K. (Müll.Frib.) 1951–1958. Die Lebermoose Europas. Dr. L. Rabenhorst's Kryptogamen-Flora 6, edn 3.
- NEES AB ESENBECK, C.G. 1838. Naturgeschichte der europäischen-Lebermoose 4. Breslau.
- PEROLD, S.M. 1999a. Studies in the liverwort genus Fossombronia (Metzgeriales) from southern Africa. 10. Three new species from Northern and Western Cape. Bothalia 29: 83–93.
- PEROLD, S.M. 1999b. Studies in the Sphaerocarpales (Hepaticae) from southern Africa. 1. The genus *Monocarpus* and its only member, *M. sphaerocarpus*. *Bothalia* 29: 225-230.

- PROSKAUER, J. 1954. On Sphaerocarpos stipitatus and the genus Sphaerocarpos. Journal of the Linnean Society of London, Botany 55: 143-157.
- PROSKAUER, J. 1955. The Sphaerocarpales of South Africa. The Journal of South African Botany 21: 63-75.
- SCHIFFNER, V. 1893. Hepaticae (Lebermoose). In H.G.A. Engler & K.A.E. Prantl (1909). Die natürlichen Pflanzenfamilien, edn 1, 1.3: 3-141 [publication date Sept. 1893 fide Stafleu & Cowan, Taxonomic literature 5: 151 (1985)].
- SCHUSTER, R.M. 1992. The Hepaticae and Anthocerotae of North America 5: 798-827. Field Museum of Natural History, Chicago.
- SCOTT, G.A.M. 1985. Southern Australian liverworts. Australian Flora and Fauna Series, No. 2.
- SÉRGIO, C. & SIM-SIM, M. 1989. Sphaerocarpos stipitatus Bisch. ex Lindenb. na Europa. Espécie introduzida em Portugal desde o século passado. Notulae bryoflorae lusitanicae III. Portugaliae Acta Biologica, Série B, 15: 414–416. STEPHANI, F. 1899. Species hepaticarum 1. Bulletin de l'Herbier
- Boissier 7. Genève.