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

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**Keywords.** *Austrosphaerocarpus* (subgenus), Hepaticae, Monocarpineae, Riellineae, southern Africa, Sphaerocarpaceae, Sphaerocarpales, Sphaerocarpineae. *Sphaerocarpos stipitatus*

**ABSTRACT**

A taxonomic account of the genus *Sphaerocarpos*, subgenus *Austrosphaerocarpus*, 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.


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 1978), 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.


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 (*Sphaerocarpaceae*); otherwise aquatic, semifrondose, stems ± 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 involucres, 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 *Riellineae* borne on archegonophores, otherwise individually surrounded by large, flask-shaped or pyriform involucres, dorsally on, or along stems of female plants. *Stalk* variable in length, without rhi-
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—subapical and pouch-like or dorsiventrally flattened with lateral, leaf-like lobes; cells uniform, all lacking oil bodies; spores single or in tetrads

1b Plants aquatic; distribution in both winter and summer rainfall regions of southern Africa; uniform in appearance, consisting of erect stem, dorsally bearing undulate wing and small leaf scales at sides and ventrally; cells dimorphic, some with an oil body; spores single, ornamentation various


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.

Diocious, heterothallic, male gametophytes much smaller than female ones. Antheridia individually developed inside small, unistratose, brownish purple, flask-like 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 sub-spherical foot, disintegrating when spores reach maturity, ornamentation finely tuberculate. Spores in local species remaining in tetrads, ornamentation ridged suborder Monocarpineae sensu Carr

2b Plants dioicous, heterothallic, male plants very much smaller than females, stems dorsiventrally flattened, laterally divided into unistratose, leaf-like lobes, without air chambers and air pores; gametangia surrounded by small or large (depending on sex) flask-shaped involucres; spores in local species remaining in tetrads, ornamentation ridged suborder Sphaerocarpineae Cavers

SB. Aggeles; 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 subgenera of Sphaerocarpus

1a Sporophytes delicate, sessile on stem or axis; wall of flakes uninistratose, without cells projecting as processes on their inner surfaces subgenus Sphaerocarpus

1b Sporophytes firm, stipitate, but length of stalk variable, wall of flakes bistratose, with inner surface bearing inward-projecting, finger-like cells, rich in chloroplasts subgenus Aastraerocarpus R.M.Schust.


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

Sphaerocarpos Adanson: 15 (1763) [oth. var.]; Steph.: 655 (1899); Müll.Frib.: 310 (1951-1958).

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

Diocious, 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).

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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 ± 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 μm 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*.

*Sphaerocarpus stipitatus* Bisch. ex Lindenb., Verhandlungen der kaiserlichen Leopoldinisch-carolinischen deutschen Akademie der Naturforscher 10 (= Nova acta Academiae Caesareae Leopoldinae Carolinicae 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, holotype).

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

*Sphaerocarpus berterii* 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 furtively branching and forming partial rosettes; markedly heterothallic, male gametophytes tiny (Figure 1A, B), Dioicous. *Female plants* pseudodichotomously branching 1–3 times, forming partial rosettes, 4.5–6.5 mm across, sometimes segments simple (Figure 1E) or nearly so, ± 4.4 × 2.6 mm, lateral leaf-like lobes (Figure 1F–M) mostly single, occasionally bilobed, obovate, size variable, 1075–2500 × 625–3375 μm above, narrower below, 275–1125 μm wide; cells at upper margin (Figure 1N) usually isodiametric, 55.0–57.5 × 50.0–62.5 μm, thin-walled, sometimes cell projecting at angle much larger, ± 52.5 × 145 μm, cells at lateral margin 87.5–125.0 × 30.0–42.5 μm; upper laminar and median cells long-hexagonal, 92.5–200.0 × 50–70 μm, basal cells 155.0–177.5 × 55–105 μm. *Archegeonal 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 involucral ring of 16 or more hyaline cells, 100–105 × 50–60 μm, rounded above and projecting somewhat crenately; rarely, larger involucres containing 2 sporophytes (Figure 2F), 3625 μm high, at mouth ± 625 μm 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 × 40–42.5 μm, 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 × 32.5 μm 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 × 40–60 μm, inner cells in 4 rows, ± 75 × 75 μm. *Calyptra* remaining unruptured for a long period enveloping mature capsule, seta and foot (Figure 2M) hyaline, mostly unistratose, cells 4–6-sided, 65–145 × 65–100 μm, smaller above, where crowned by persistent archegonial neck (Figure 2N) and below, where closely investing seta and foot, here up to 4-stratose. *Archegeonal neck* 75–85 × 30.0–37.5 μm, formed by 6 rows of cells and reportedly (Schuster 1992) with only 2 neck-canals. *Capsule* 650–825 μm diam., wall (Figure 2Q) unistratose, lacking thickenings, cells ± 5-sided, 37.5–65.0 × 37.5–50.0 μm, densely covered with starch granules, particularly when young; with age their number apparently reduced, subround or oval, 5.0–12.5 × 5–10 μm. *Seta* (Figure 2O) with 4 cell rows, very short, ± 100 × 40 μm, becoming necrotic. *Foot* partly fused with calyptra below, bulbous, ± 270 × 220 μm, resting on 'platform' of cells filling basal part of flask, cells 100–170 × 75–125 μm; in cross section (Figure 2P) centrally with several 'haustorial' cells, roughly triangular, corners rounded, ± 42.5 μm long, up to 47.5 μm wide across widest part, surrounded by thin layer of non-cel- lular tissue and then by 2 or 3 rows of hyaline cells, the largest, outermost cells 30.0–37.5 × 32.5–37.5 μm. *Spores* remaining in tetrads, 87.5–112.5 μm diam., yellow-brown to dark brown; 3 (Figure 4C) or all 4 spores (Figure 3A, B, D, E) of tetrad visible at the same time, joined at thin line in narrow groove (Figure 4F), ± 2.5 μm wide, ornamentation ridged, with 16–19 minutely
papillate ridges, sometimes branched and up to 10 μm 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 μm, 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. R₁–R₅, nutritive cells. A–R₅, Koekemoer 1425. Scale bars: A–C, L, P, 50 μm; D–F, 500 μm; G–K, 100 μm; M, N, 200 μm; O, Q, R₁–R₅, 25 μm. Artist: Gillian Condy.
Bothalia 30,1 (2000)

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 *Sphaerocarpus* 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 ± 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**

<table>
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<tr>
<th>Specimen</th>
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<tr>
<td>Britten 58348</td>
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<td>Koekemoer 1425</td>
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<td>Magell &amp; Schelpe 3961A</td>
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<td>Oliver 8961</td>
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<td>Pernold 1838</td>
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<td>A.S.L. Schelpe 760</td>
<td>(BOL58344)</td>
<td>EACLE  Schelpe 4877</td>
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<td>Toelken 1978</td>
<td>(BM)</td>
<td>BOL58347 (ridges rather thicker in the spores from this specimen, see Figure 4B).</td>
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FIGURE 5 — Distribution of *Sphaerocarpos stipitatus* in southern Africa. Pocock specimen not indicated on map (grid reference 3326AD), because I did not examine it.


