

# Studies in the Sphaerocarpaceae (Hepaticae) from southern Africa. 3. The genus *Riella* and its local species

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**Keywords:** Hepaticae, *Riella* Mont., *R. affinis* M.Howe & Underw., *R. alatospora* Wigglesworth, *R. capensis* Cavers, Riellaceae Engl., *R. echinospora* Wigglesworth, *R. purpureospora* Wigglesworth, Riellineae R.M.Schust., southern Africa, Sphaerocarpaceae Cavers, subgenus *Riella*, subgenus *Trabutiella* Porsild

## ABSTRACT

A taxonomic account of the aquatic liverwort genus *Riella* Mont., its two subgenera and five local species is presented. This comprises descriptions and illustrations of these taxa together with a distribution map and a key to the subgenera and species. The taxa are classified in the order Sphaerocarpaceae Cavers, suborder Riellineae R.M.Schust. A description of the order Sphaerocarpaceae and a key to the three local suborders are given in Perold (2000) in the present series.

## INTRODUCTION

The genus *Riella* Mont. was first recorded from southern Africa by Cavers (1903). Dried mud, containing crustacea, the *raison d'être* for its collection, was taken from a shallow pond near Port Elizabeth, Eastern Cape, in 1897 by a Mr Hodgson and sent to Owens College, Manchester (via Plymouth), where it was placed in a small aquarium. In a few weeks a number of green shoots had grown out of the mud. Upon fruiting, they were recognized as hepatics and sent to Cavers at Yorkshire College, Leeds. He identified and described them as a new species, *R. capensis*.

In 1926 and 1932 Miss E.L. Stephens sent a number of South African *Riella* plants together with algae and samples of mud to Manchester. Three new species of *Riella* from the Cape were isolated, one of which was from Valkenberg Vlei, unfortunately without ripe spores. A fourth species was from Schonken's Salt Pan near Brandfort in the Free State. These species were studied and described by Wigglesworth (1937). Her descriptions were subsequently supplemented by Proskauer (1954), who also identified a Pocock specimen from a farm dam, 4 miles (6.4 km) from Grahamstown, as the widely distributed *R. affinis*, thus adding a fifth species to the southern African records of *Riella*. Arnell (1957, 1963) did not record any new species, but listed two new collections from Namibia, the whereabouts of which have not been traced. Unfortunately, very few collections have been made in the last 30–40 years.

The occurrence of these plants is stated to be rare and sporadic, which can perhaps be attributed to the fact that minor changes in the environment can result in their disappearance (Schuster 1992). Rapid urbanization in southern Africa in recent years, has also led to the destruction of natural habitats, particularly on the Cape Flats.

The gametophytes of *Riella* are delicate, short-lived and highly susceptible to differing environmental conditions, which, if not leading to their disappearance, may cause major changes in their size and form. The spores, however, are exceedingly resistant, surviving in the dried state for years. With ornamentation that is regarded as species-specific, spores are essential for identification, as few *Riella* species show well-marked, distinguishing vegetative characters. Sometimes only the mode of branching may be of some significance. This study was undertaken, even in the absence of recent collections, because information gained by means of newer techniques such as SEM micrographs of the spores (and thalli) of southern African species has not been published before. It also completes this series of studies in the local Sphaerocarpaceae, which were excluded in my treatment of the Marchantiidae for the *Flora of southern Africa* (Perold 1999a).

## 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.

Throughout this treatment of the Sphaerocarpaceae and Riellaceae I have used the term 'stem', although it is usually referred to as 'axis' or 'rib'. Some of the species descriptions and illustrations of *Riella* provide rather less detail than others, because of a lack of suitable material.

Differences and similarities between the five southern African *Riella* species are presented in tabular form (Table 1).

A description of the order Sphaerocarpaceae and a key to the three local suborders, i.e. Monocarpineae, Sphaerocarpaceae and Riellineae, are provided in the previous article, no. 2 (Perold 2000), in the present series.

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TABLE 1.—Comparison of southern African *Riella* species

	<i>R. affinis</i>	<i>R. alatospora</i>	<i>R. capensis</i>	<i>R. echinospora</i>	<i>R. purpureospora</i>
Plant length	up to 23 mm	20–35 mm	10–30 mm	up to 35 mm	20–60 mm
Wing width	2.4–3.0 mm	1.8–3.4 mm	1.5–2.8 (–4.0) mm	1.6–2.1 mm	1.3–2.75 $\mu$ m
Stem in cross section	155–175 $\times$ 200–255 $\mu$ m	350–400 $\times$ 280–300 $\mu$ m	200–300 $\times$ 300–350 $\mu$ m	150–225 $\times$ 230–250 $\mu$ m	330–350 $\times$ 350–380 $\mu$ m
Lateral leaf scales	540–730 $\times$ 100–150 $\mu$ m	400–720 $\times$ 410–720 $\mu$ m	430–750 $\times$ 360–800 $\mu$ m	400–510 $\times$ 160–350 $\mu$ m	570–925 $\times$ 310–800 $\mu$ m
Ventral leaf scales	350–400 $\times$ 170–190 $\mu$ m	160–280 $\times$ 180–400 $\mu$ m	300–380 $\times$ 310–330 $\mu$ m	similar to above	270–450 $\times$ 320–480 $\mu$ m
Sexual state	monoicous; protandrous	dioicous	dioicous	dioicous	dioicous
Involucre					
size	1575–1700 $\times$ 900–1000 $\mu$ m	up to 2125 $\times$ 1450 $\mu$ m	1875–2675 $\times$ 1050–1350 $\mu$ m	1375–1675 $\times$ 950–1050 $\mu$ m	2375–2575 $\times$ 1600 $\mu$ m
shape	ellipsoid-ovoid	obovoid	ovoid-acuminate	ovoid, sometimes acuminate	pyriform
beak	gradually contracted, occluded	narrowing, encircled by $\pm$ 13 cells	long drawn out	tapering, sometimes occluded	abruptly narrowed
ribbed or smooth	8-ribbed	$\pm$ smooth	$\pm$ smooth	$\pm$ smooth	$\pm$ smooth
Stalk	very short, oblique	fleshy, $\pm$ 350 $\times$ 350–430 $\mu$ m	500–625 $\times$ 150–175 $\mu$ m	$\pm$ 375 $\times$ 270 $\mu$ m	$\pm$ 375 $\times$ 250 $\mu$ m
Seta length	$\pm$ 150 $\mu$ m	very short, 50–60 $\mu$ m	275–350 $\mu$ m	$\pm$ 100 $\mu$ m	$\pm$ 210 $\mu$ m
Foot shape	bulbous	uniform along its length	gradually widening below	uniform along its length	gradually widening below
Spores					
diameter	80–100 $\mu$ m	105–125 $\mu$ m	95–120 $\mu$ m	87.5–97.5 $\mu$ m	82.5–117.5 $\mu$ m
colour	light brown	golden brown	light brown	light brown	purple (or red)
wing	absent	present, $\pm$ 20 $\mu$ m wide	absent	absent	absent
shape	subglobose	$\pm$ triangular	$\pm$ triangular	subglobose	$\pm$ triangular
ornamentation of distal face	$\pm$ 11 irregular rows of spines across	$\pm$ 11 or 12 irregular rows of spines across	10–12 rows of spines across	13–16 irregular rows of spines across	$\pm$ 12 rows of spines across
at periphery/margin	$\pm$ 36 spines projecting at periphery	$\pm$ 32 spines projecting at margin	30–36 spines projecting at margin	50 or more spines projecting at periphery	25–30 spines projecting at margin
length of spines	7.5–12.5 $\mu$ m	5.0–7.5 $\mu$ m	10–12 $\mu$ m	up to 10 $\mu$ m	7.5–10.0 $\mu$ m
apices of spines	truncate	dilated, truncate	acute, sometimes blunt	slender, acute, rarely swollen	stout, truncate
basal membranes	faint, reticulation imperfect	reticulation indistinct	reticulation indistinct	absent to weakly reticulate	irregular reticulation
ornamentation of proximal face	spines, small and fine, $\pm$ 2.5 $\mu$ m long	papillae irregular, granules at margin	papillae and tiny granules; marginal webbing	small, fine spines	$\pm$ 15 low spines per facet, marginal webbing prominent
triradiate mark	absent	absent	faint	absent	present, complete or partial

Suborder **Riellineae** *R.M.Schust.*: 32 (1958); *R.M.Schust.*: 827 (1992).

Plants aquatic, usually entirely submerged, thallus developing in vertical plane, bilaterally symmetrical in plane of wing, secondarily asymmetrical. *Stem* (or axis) slender, erect, elongate, simple or furcate, in section ellipsoid or subround, invested with unistratose wing along its dorsal side. *Wing* undulate or ruffled, thin, over-arching stem at coiled apex. *Scales* unistratose, leaflike, mostly dimorphic, the two forms not always easy to distinguish: lateral leaf scales basally attached to stem and formed at juncture of wing and stem, at maturity on both sides of wing and often associated with young involucres; ventral leaf scales produced along ventral surface of stem, smaller and often constricted in middle, with laminar attachment to stem by single cell or row of cells. *Cells* thin-walled, here and there with a single oil body. *Rhizoids* generally only borne basally on stem, all smooth-walled.

Asexual reproduction by gemmae from ventral side of stem and similar to ventral leaf scales.

Dioicous or rarely monoicous. *Antheridia* individually developed along thickened, free margin of wing, sunken in pockets, ovoid, on very short pedicel. *Archegonia* single, when fertilized enclosed in flask-shaped involucres, smooth or rarely fluted with parallel, longitudinal ribs or lamellae, in acropetal sequence, usually to right and left of wing. *Sporophyte* with globose capsule, short seta and spherical or  $\pm$  uniformly wide foot, cleistocarpous; spores released on decay of capsule wall and involucre. *Spores* large, single, not permanently united in tetrads, brown or purple to red; distal face ornamented with fine or coarse spines, tips truncate, sometimes wider below and basally connected by membranes, rarely with prominent wing; proximal face with few to many, finer spines. *Nutritive cells* present, 4-nucleate. *Elaters* absent.

**Riellaceae** *Engl.* in *Syllabus der Pflanzenfamilien*, edn 1: 45 (1892); *Schiffn.*: 51 (1893) as *Rielloideae*; *Müll.Frib.*: 314 (1951–1958); *S.W.Arnell.*: 6 (1963); *R.M.Schust.*: 836 (1992).

The Riellineae include only the family Riellaceae; hence the details are not repeated in the subordinal description.

**Riella** *Mont.* in *Annales des Sciences Naturelles*, Sér. 3, Bot. 18: 11 (1852); *Müll.Frib.*: 314 (1951–1958); *R.M.Schust.*: 836 (1992). Type: *R. notarisii* (Mont.) Mont.

*Duriaea* *Bory & Mont.*: 1115 (1843), not of Mérat: 432 (1829).

*Maisonmeuva* *Trevis.*: 442 (1877).

Plants green, aquatic, erect in growth, 10–60 mm tall. *Stem* (or axis) sparsely branched, slender, invested along dorsal side with undulate or ruffled wing and on each

side with lateral leaf scales and ventrally with smaller, ventral leaf scales. *Rhizoids* usually only at base of stem, hyaline, smooth.

Dioicous or rarely monoicous. *Antheridia* in pockets along free wing margin. *Archegonia* in flask-shaped involucres, smooth or rarely with longitudinal ribs or lamellae. *Sporophyte* globose. *Spores* not remaining in tetrads, large, 100–120  $\mu$ m diam.

*Riella* is unique among Hepaticae in that there is an intermediate stage in thallus development, i.e. the juvenile stage, in which growth is initiated by an intercalary meristem (Thompson 1941).

#### Key to two subgenera and locally occurring species of *Riella*

- 1a Involucral flasks surrounding sporophytes with 8, or sometimes more, longitudinal 'ribs' or lamellae; plants monoicous, widespreading; spores light brown, subglobose . . . . . subgenus *Trabutiella* Porsild (= section *Plicatae* Allorge)
  - 1. *R. affinis*
- 1b Involucral flasks surrounding sporophytes smooth, without 'ribs' or lamellae; plants dioicous, endemic to South Africa; spores brown or purple to crimson, triangular or subglobose . . . . . subgenus *Riella* (= section *Euriella* Porsild and section *Laevigatae* Allorge):
  - 2a Spores brown, with or without wings:
    - 3a Spores winged . . . . . 2. *R. alatospora*
    - 3b Spores without wings:
      - 4a Spores triangular; involucre ovoid, long-acuminate, capsule occupying its lower  $\frac{1}{2}$  . . . . . 3. *R. capensis*
      - 4b Spores subglobular; involucre ovoid, shortly acuminate, capsule occupying its lower  $\pm \frac{3}{4}$  . . . . . 4. *R. echinospora*
  - 2b Spores purple or crimson, marginal webbing prominent . . . . . 5. *R. purpureospora*

Subgenus **Trabutiella** *Porsild* in *Botanisk Tidskrift* 24: 323 (1902).

1. ***Riella affinis*** *M. Howe & Underw.* in *Bulletin of the Torrey Botanical Club* 30: 221 (1903); *R.H.Thomps.*: 110 (1940); *ibid.*: 845 (1941); *ibid.*: 275 (1942); *Prosk.*: 69 (1955); *S.W.Arnell.*: 7 (1963); *Magill & Schelpe.*: 9 (1979). Type: on bank of a reservoir, Tafira, Grand Canary, June 1897, *O.F. Cook* 729 (US, Smithsonian Inst., presumed iso., fide *Prosk.*).

*R. vishwanatai* *Pandé et al.*: 166 (1954). Type: India, Lake Latif Shah, Uttar Pradesh. *Misra* 3590. Synonymy fide *Prosk.* (1954).

Plants erect (Figure 1A, B) or semi-erect, wholly submerged or sometimes partly exposed, delicate, up to 23 mm tall, stems simple or sparsely furcate, occasionally with adventitious branching toward base, the latter generally attached to substrate by rhizoids. *Stem* slender, in cross section (Figure 1C) slightly flattened on dorsal side, rounded on ventral side, 155–175  $\mu$ m or  $\pm$  8 cell rows thick, 200–255  $\mu$ m wide, outer cells small,  $\pm$  ovoid, 12.5–17.5  $\times$  22.5–27.5  $\mu$ m, inner cells somewhat larger, angular, 30.0–37.5  $\times$  20.0–37.5  $\mu$ m. *Wing* unistratose, with margin entire, overarching stem apex and rounded above, 2.4–3.0 mm wide, narrowing below and undulate, gradually disappearing toward base, becoming deeply notched at sinuses (Figures 1A, B; 2A), containing 1 or

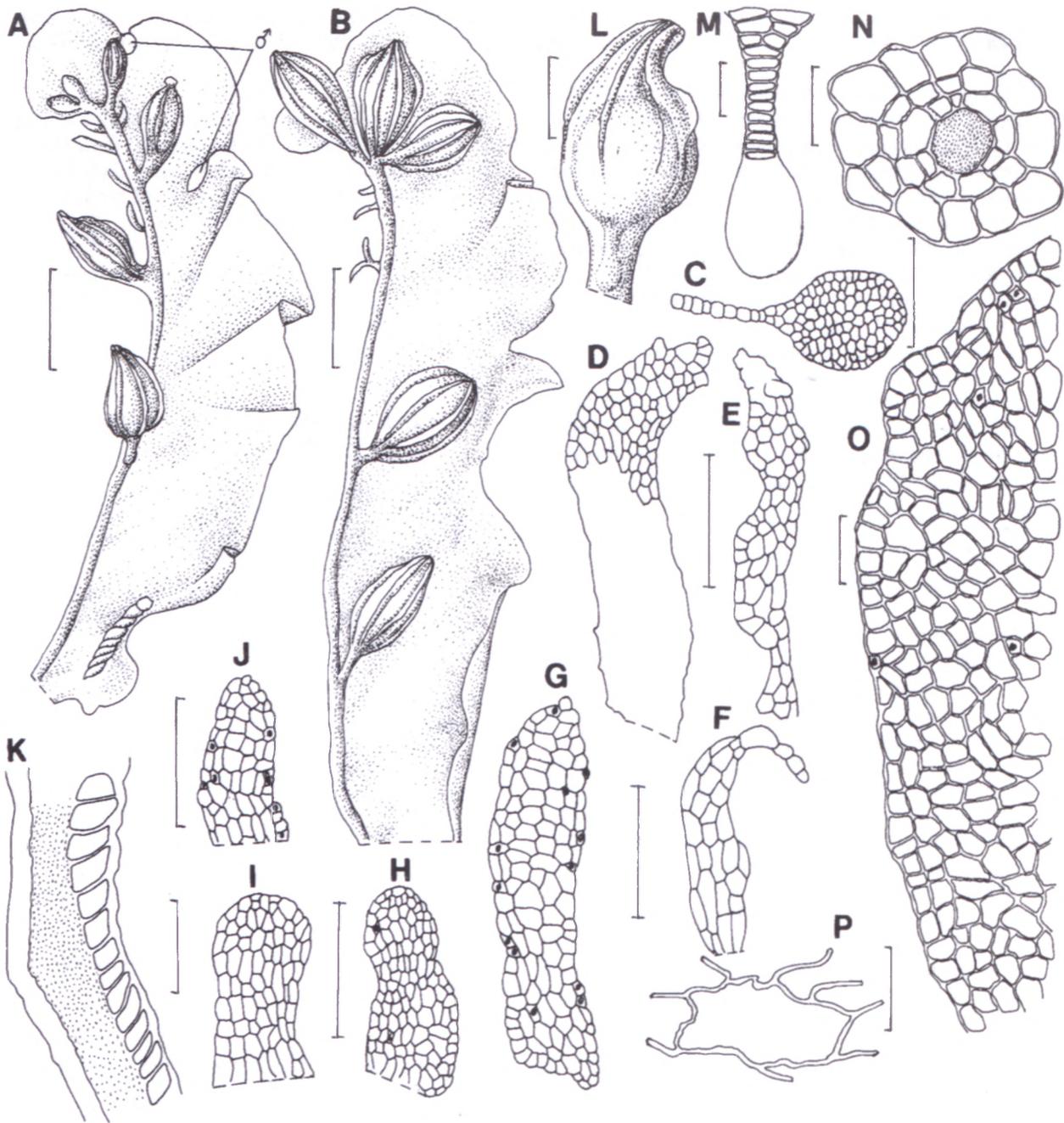


FIGURE 1.—*Riella affinis*, Pocock BOL20503. A, B, monoicous plants seen from side, with involucre (containing capsules) in acropetal sequence along stem; at wing margin, antheridia (indicated by ♂) 1 or 2(3) in notches or more numerous in a row, side by side; C, c/s stem and part of wing. D–G, lateral leaf scales [G, after Thompson (1941) with smaller cells containing a single oil body]. H–J, ventral leaf scales [J, after Thompson (1941)]. K, much enlarged row of antheridia at margin of narrowed part of wing; L, sporophyte with enveloping involucre and calyptra; M, surface view of seta, upper part up to 4-stratose, below unistratose, supported on bulbous foot; N, c/s calyptra surrounding upper part of seta; O, detail of involucre rib (one of 8–10); P, c/s involucre wall (rather flattened) with ribs. Scale bars: A, B, 2 mm; C, 200  $\mu$ m; D–J, 250  $\mu$ m; K, L, P, 500  $\mu$ m; N, 50  $\mu$ m; O, M, 100  $\mu$ m.

more antheridial involucre; cells near stem 5- or 6-sided,  $87.5\text{--}112.5 \times 27.5\text{--}50.0 \mu\text{m}$ , near margin smaller, mostly 4-sided,  $27.5\text{--}35.0 \times 25\text{--}45 \mu\text{m}$ . Scales dimorphic: lateral leaf scales (Figure 1D–G) at juncture of wing and stem, often associated with archegonia or young involucre,  $\pm$  regularly distributed along both sides of stem, unistratose, linear-lanceolate or tapering apically,  $540\text{--}730 \times 100\text{--}150 \mu\text{m}$ , marginal cells 4- or 5-sided,  $17.5\text{--}35.0 \times 17.5\text{--}20.0 \mu\text{m}$ , smaller ones sometimes containing an oil body, cells in body angular,  $25\text{--}60 \times 22.5\text{--}37.5 \mu\text{m}$ ; ventral leaf scales (Figure 1H–J) obliquely attached to morphological ventral side of stem, fewer and smaller than lateral leaf scales, often constricted in middle,  $350\text{--}400 \times 170\text{--}190$

$\mu\text{m}$ , marginal cells  $\pm$  rectangular in shape,  $12.5\text{--}25.0 \times 7.5\text{--}12.5 \mu\text{m}$ , some smaller ones with an oil body, cells in scale body 4–6-sided,  $32.5\text{--}35.0 \times 20\text{--}25 \mu\text{m}$ . Rhizoids arising from base, or along length of stem, hyaline, smooth,  $20\text{--}30 \mu\text{m}$  wide.

Asexual reproduction reportedly by gemmae, but not seen in present investigation; said to develop periodically along stem and to be similar to ventral scales.

Monoicous and protandrous. Antheridia discharged in specimens examined, involucre flask-shaped,  $\pm 250 \times 120 \mu\text{m}$ , pockets variable in number, discontinuous along

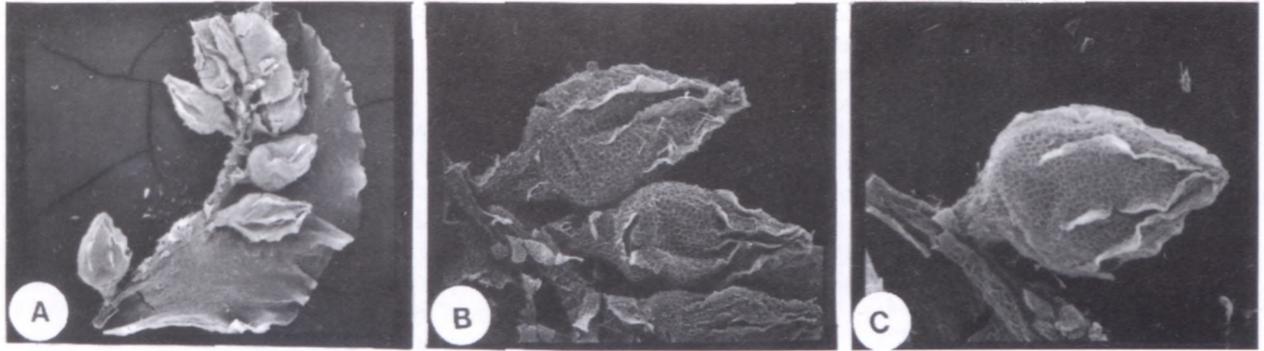


FIGURE 2.—*Riella affinis*, Pocock BOL20503. SEM micrographs of plants. A, stem of plant with wing and ribbed female involucre; B, several involucre; C, single involucre. A,  $\times 8.3$ ; B, C,  $\times 25.6$ .

wing margin, if only 1 or 2(3), then in notches (Figure 1A, B) at irregular intervals, otherwise in a row (Figure 1A, K), with as many as 13 lying side by side, ducts oblique, up to  $\pm 125 \mu\text{m}$  long, opening through pores at wing edge, width of wing here reduced (Figure 1K). *Archegonia* borne on dorsal surface of stem, on either side at join with wing, in acropetal sequence. *Involucre* (Figures 1L; 2A–C) up to 8 or even 10, along stems, ellipsoid-ovoid, ribbed,  $1575\text{--}1700 \mu\text{m}$  long,  $900\text{--}1000 \mu\text{m}$  wide across middle, including ribs, gradually contracted and eventually occluded at beak, also narrowed toward base, ribs (Figure 1O) mostly 8 in number (Figure 1P), joined at apex, unistratose, undulate, almost as long as involucre,  $110\text{--}160 \mu\text{m}$  wide across central, widest part, narrower above and below, cells 4–6-sided,  $30.0\text{--}42.5 \times 20\text{--}25 \mu\text{m}$ , at entire margin rectangular,  $25\text{--}45 \times 15.0\text{--}17.5 \mu\text{m}$ , cells in involucre wall densely chlorophyllose, 4–6-sided,  $35\text{--}50 \times 30.0\text{--}37.5 \mu\text{m}$ . *Stalk* very short, obliquely inserted on stem, internally occupied by seta and foot, as well as surrounding 3- (or 4-)

stratose, basal calyptra wall, and externally covered by lower part of involucre wall. *Calyptra* closely investing mature capsule, hyaline, outer cells in surface view, 6- or 7-sided,  $60.0\text{--}82.5 \times 40\text{--}50 \mu\text{m}$ , crowned above by archegonial neck, below closely surrounding seta and foot; in cross section (Figure 1N) cells in outer row larger,  $20\text{--}25 \times 32.5\text{--}37.5 \mu\text{m}$ , in central row,  $12.5\text{--}20.0 \times 25 \mu\text{m}$ , in innermost row  $12.5\text{--}15.0 \times 15\text{--}20 \mu\text{m}$ . *Archegonial neck*  $\pm 100 \times 37.5 \mu\text{m}$ , upper part purple, below colourless, with 6 rows of cells and 4 neck canal cells. *Capsule* ovoid to subglobose,  $750\text{--}800 \mu\text{m}$  diam., wall unistratose, thickenings absent, cells  $\pm$  rectangular,  $50.0\text{--}67.5 \times 35\text{--}50 \mu\text{m}$ . *Seta* (Figure 1M)  $\pm 150 \mu\text{m}$  long, dark red, upper end wider, 3- or 4-seriate, below  $\pm 37.5 \mu\text{m}$  wide, uniseriate, soon becoming necrotic. *Foot* bulbous, multicellular,  $150\text{--}170 \times 140 \mu\text{m}$ , in cross section with large, closely packed, roughly triangular, haustorial cells,  $55\text{--}70 \times 27.5\text{--}35.0 \mu\text{m}$ , closely surrounded by 3- or 4- stratose base of calyptra. *Spores*  $80\text{--}100 \mu\text{m}$  diam., including spines, light brown, without wing, subglobose;

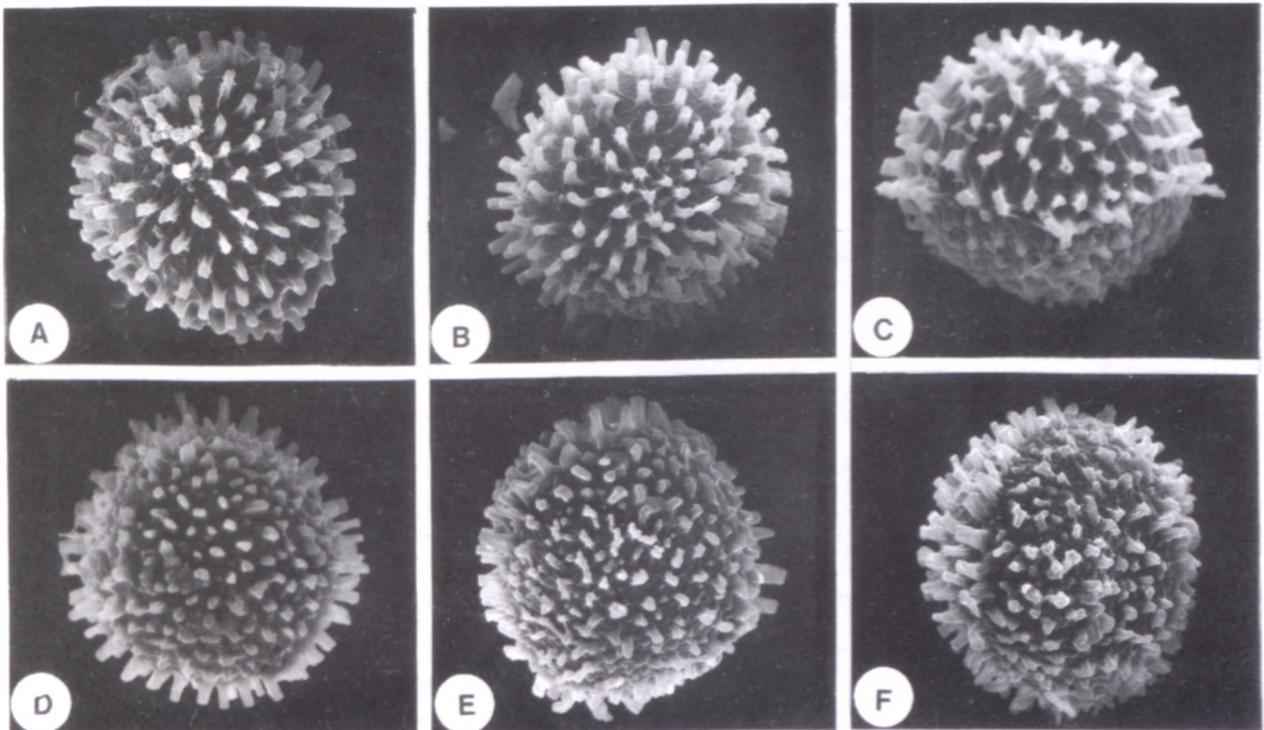


FIGURE 3.—*Riella affinis*, Pocock BOL20503. SEM micrographs of spores. A, B, distal face; C, lateral view of part of distal face above and proximal face below; D, E, proximal face; F, proximal face, with shorter spines, seen slightly from side, exposing larger spines of distal face on the right. A,  $\times 373$ ; B,  $\times 361$ ; C,  $\times 418$ ; D,  $\times 350$ ; E,  $\times 407$ ; F,  $\times 441$ .

distal face (Figure 3A–C) densely covered with  $\pm 11$  irregular rows of spines across diam. and  $\pm 36$  projecting at periphery, 7.5–12.5  $\mu\text{m}$  long, apices blunt, truncate, rarely acute, basal membranes interconnecting spines below quite faint, sometimes forming imperfect reticulations; proximal face (Figure 3D–F) with triradiate mark absent, spines small and fine,  $\pm 2.5$   $\mu\text{m}$  long, not basally interconnected. *Nutritive cells* no longer present in material examined. *Spore release* by disintegration of capsule wall, then of calyptra and finally of involucre wall.

#### DISCUSSION

*Riella affinis* is a widely dispersed species, originally known from Grand Canary; then from Stanford University campus, California; Uttar Pradesh, India (as *R. vishwanatai*); near Grahamstown, South Africa (Figure 4), and finally, from Israel (unpublished, according to Lipkin & Proctor 1975). Schuster (1992) states that it was also reported from Argentina by Hässel de Menéndez (1959), but this is incorrect, as *R. affinis* is not mentioned in this paper, which deals with *R. americana* M. Howe & Underw.

On account of its ribbed involucre, *R. affinis* is easily recognised and has been placed in subgenus *Trabutiella*, together with two other species from elsewhere, but it is the only monoicous one. The two other species are *R. cossoniana* Trabut (= *R. paulsenii* Porsild, placed in synonymy by Lipkin & Proctor 1975) and *R. garnundiae* Hässel de Menéndez.

Schofield (1985: fig. 15–2A, B) illustrates what he calls *Riella affinis*. 'A' is of an 'antheridium-producing gametophore' and 'B', 'detail of marginal chambers with antheridia'. He cites Wigglesworth (1937) as his source for A and B. 'A' is actually an enlargement of Wigglesworth's fig. 49 of a male plant of *R. echinospora* Wigglesworth, whereas his 'B' is an exact copy of her fig. 51 of the same species. Schofield does not cite a source for his 'C', which illustrates a 'sporophyte-bearing gametophore'; the involucre is, however, without ribs. It should be emphasized here, that Wigglesworth

(1937) did not treat *R. affinis*, as it was first collected in South Africa in 1953 by Pocock and recorded by Proskauer (1954).

Thompson (1942) refers to 'explosive discharge of the antherozoids' in both culture and in temporary mounts, but Proskauer (1955) comments that he had never observed explosive discharge of antheridia in *Riella*. Proskauer also found wider variation in spore size, 70–130  $\mu\text{m}$  diam., than I did. He remarks that, 'spore size is of limited diagnostic value in the order,' an admonition it would be well to keep in mind. Spore ornamentation, on the other hand, particularly as illustrated on SEM micrographs, is crucial to correct identification.

Proskauer (1955) reports that the specimen collected by Dr Pocock on 31 March 1953, was from 'Farm dam, 4 miles from Grahamstown on Cradock Road ... about  $\frac{1}{4}$  mile down from road'. On the label of another Pocock specimen collected on 10 May 1953 (BOL20503), this locality (Figure 4) is given as 'Dam on Table Hill Farm, Cradock Road, 6 miles'. I visited the area in October 1999 and found the name of this farm now to be 'Table Farm, Hilton' owned by the White family. I collected some mud from the bed of the Palmiet River, where the mostly dried up river runs under a bridge on the road (R350) from Grahamstown. Subsequently the techniques for cultivation, as described by Proctor (1972) and Hässel de Menéndez (1987), were followed, but without success.

#### Specimen examined

Pocock BOL20503

#### Subgenus *Riella*

*Euriella* Porsild in Botanisk Tidsskrift 24: 327 (1902).

2. *Riella alatospora* Wigglesworth in Journal of the Linnean Society of London, Botany 5: 317 (1937); Prosk.: 68 (1955); S.W. Arnell: 7 (1963); Magill & Schelpe: 9 (1979). Type: Cape Town, original locality, vlei at Salt River between main road and railway line, legit *E.L. Stephens*, atque usu sporarum illae originis coluit *G. Wigglesworth* (BOL!; MANCH!) (? type not designated).

Plants erect, 20–35 mm tall, some with stem simple, others once-furcate near base and bilateral, with 2 nearly equal shoots connected below by intermediate membranous portion (Figure 5A), occasionally with clusters of branches, possibly developed from numerous adventitious shoots. *Stem* (Figure 5D) in cross section  $\pm$  ovoid or slightly flattened dorsally and rounded ventrally, 350–400  $\mu\text{m}$  or 9 cell rows thick, 280–300  $\mu\text{m}$  wide, outer cells rectangular or isodiametric, rather smaller, 25–50  $\times$  22.5–37.5  $\mu\text{m}$ , inner cells angular, 50–60  $\times$  42.5–50.0  $\mu\text{m}$ . *Wing* unistratose, sometimes bistratose at join with stem, margin slightly eroded, overarching stem apex, 1.8–3.4 mm wide, undulate, narrowing below and soon disappearing; cells near stem 5- or 6-sided, 62.5–95.0  $\times$  37.5–42.5  $\mu\text{m}$ , near margin smaller and mostly 4-sided.

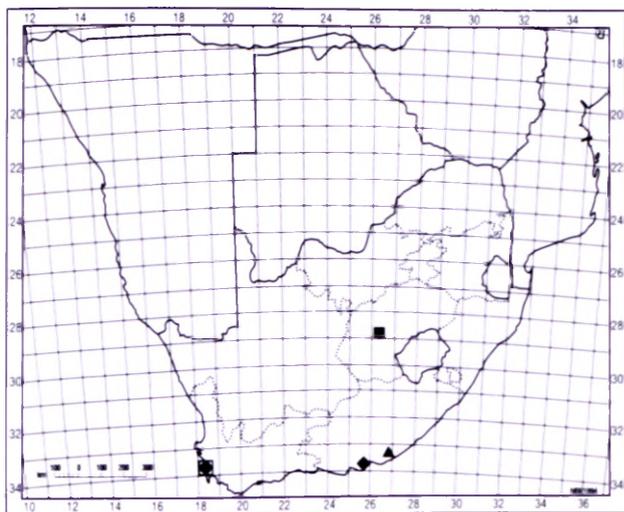


FIGURE 4.—Distribution of *Riella* species in southern Africa. A, *R. affinis*.  $\blacktriangle$ ; *R. alatospora*.  $\square$ ; *R. capensis*.  $\blacklozenge$ ; *R. echinospora*.  $\blacksquare$ ; *R. purpureospora*.  $\bullet$

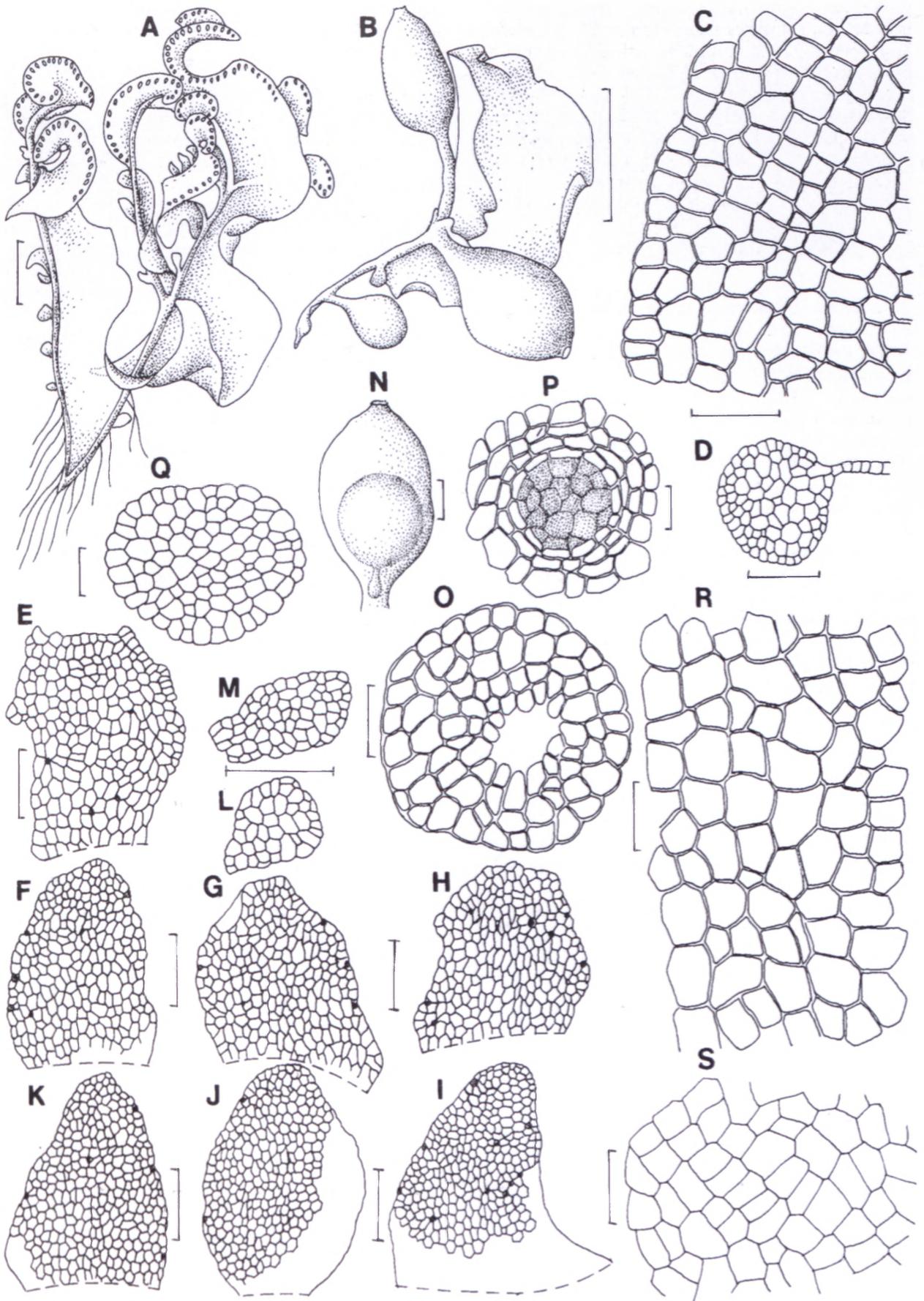


FIGURE 5.—*Riella alatospora*, E.L. Stephens BOL26400. A, male plant once furcate near base, with numerous antheridia along wing margins (after Wigglesworth 1937); B, female plant with 3 involucre; C, wing margin with several rows of smaller cells; D, c/s stem and part of wing; E–K, lateral leaf scales; L, M, ventral leaf scales; N, sporophyte with stalked involucre; O, mouth of involucre from above; P, c/s foot; Q, c/s stalk; R, surface view of cells in involucre wall; S, cells in capsule wall. Scale bars: A, B, 2 mm; C, O, P, R, 50  $\mu$ m; D, 200  $\mu$ m; E–M, 250  $\mu$ m; N, 500  $\mu$ m; Q, S, 100  $\mu$ m.

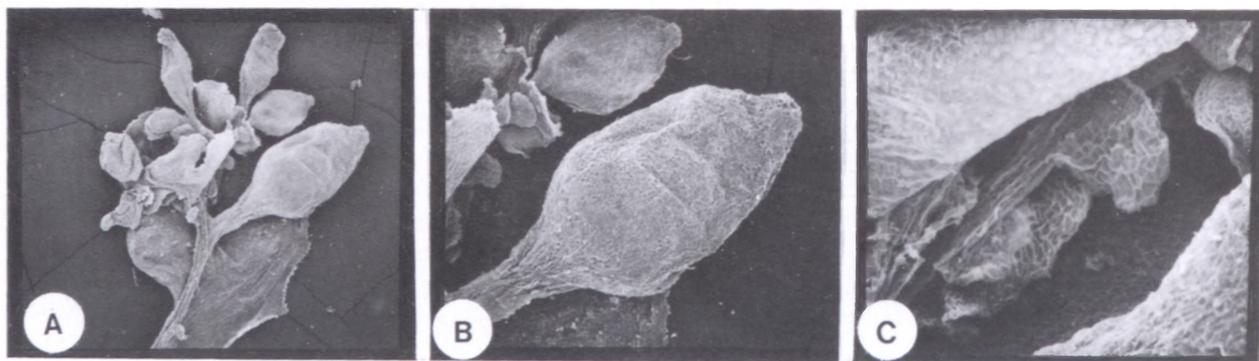


FIGURE 6.—*Riella alatospora*, E.L. Stephens BOL26400. SEM micrographs of plants. A, several involucres along stem; B, close-up view of mature involucre raised on stalk; C, leaf scales along stem. A,  $\times 8.3$ ; B,  $\times 18.4$ ; C,  $\times 45.5$ .

25–45  $\times$  22.5–25.0  $\mu\text{m}$ , sometimes outer 5, 6 or more rows (Figure 5C) without chloroplasts; several smaller cells,  $\pm 20 \times 20 \mu\text{m}$ , filled with an oil body, scattered throughout wing. *Scales* dimorphic (Figure 6C): lateral leaf scales (Figure 5E–K) often paired, regularly and obliquely attached along stem, some bluntly triangular in shape, others irregular, 400–720  $\times$  410–720  $\mu\text{m}$ , marginal cells 4- or 5-sided, 25–45  $\times$  15–30  $\mu\text{m}$ , cells in body 5- or 6-sided, 27.5–50.0  $\times$  22.5–42.5  $\mu\text{m}$ , smaller cells scattered throughout, 17.5–22.5  $\times$  17.5–22.5  $\mu\text{m}$ , each containing an oil body; ventral leaf scales (Figure 5L, M) fewer and smaller than lateral leaf scales, shape variable, 160–280  $\times$  180–400  $\mu\text{m}$ , marginal cells 4- or 5-sided, 40.0–47.5  $\times$  27.5–42.5  $\mu\text{m}$ , in between with occasional smaller, wedge-shaped cells  $\pm 25 \times 25 \mu\text{m}$  in largest dimension, containing an oil body, cells in body angular, 42.5–67.5  $\times$  37.5–45.0  $\mu\text{m}$ .

Dioicous. Male plants same size as female plants or often smaller. *Antheridia* numerous, in a single, linear

series in pockets along thickened wing margin. *Archegonia* near apex of stem, on both sides of wing. *Involucres* (Figures 5B, N; 6A, B) up to 5 produced in acropetal sequence along stem, obovoid,  $\pm$  smooth, up to 2125  $\mu\text{m}$  long, 1450  $\mu\text{m}$  wide across widest part, narrowing upwards to beak,  $\pm 175 \mu\text{m}$  wide and surrounded by as many as 13 crowded, slightly projecting cells (Figure 5O), below also contracted toward stalk, cells in unistratose involucral wall (Figure 5R) 5- or 6-sided, 42.5–57.5  $\times$  32.5–42.5  $\mu\text{m}$ . *Stalk* fleshy below, obliquely attached to stem,  $\pm 350 \times 350$ –430  $\mu\text{m}$ , in cross section (Figure 5Q) cells in outer row angular, 50–55  $\times$  30.0–47.5  $\mu\text{m}$ , inner cells  $\pm$  ovoid or angular,  $\pm 50 \times 45$ –60  $\mu\text{m}$ , foot resting on internal cells of fleshy part. *Calyptra* bi- or tristratose, outer layer of cells in surface view polygonal, 37.5–65.0  $\times$  35.0–67.5  $\mu\text{m}$ , above archegonial neck remaining attached,  $\pm 100 \times 40 \mu\text{m}$ . *Capsule* globose, 1050–1150  $\mu\text{m}$  diam., cells in wall (Figure 5S) angular, 50–80  $\times$  30–50  $\mu\text{m}$ . *Seta* very short, 50–60  $\mu\text{m}$  long, dark red, expanded above, up to  $\pm 165$

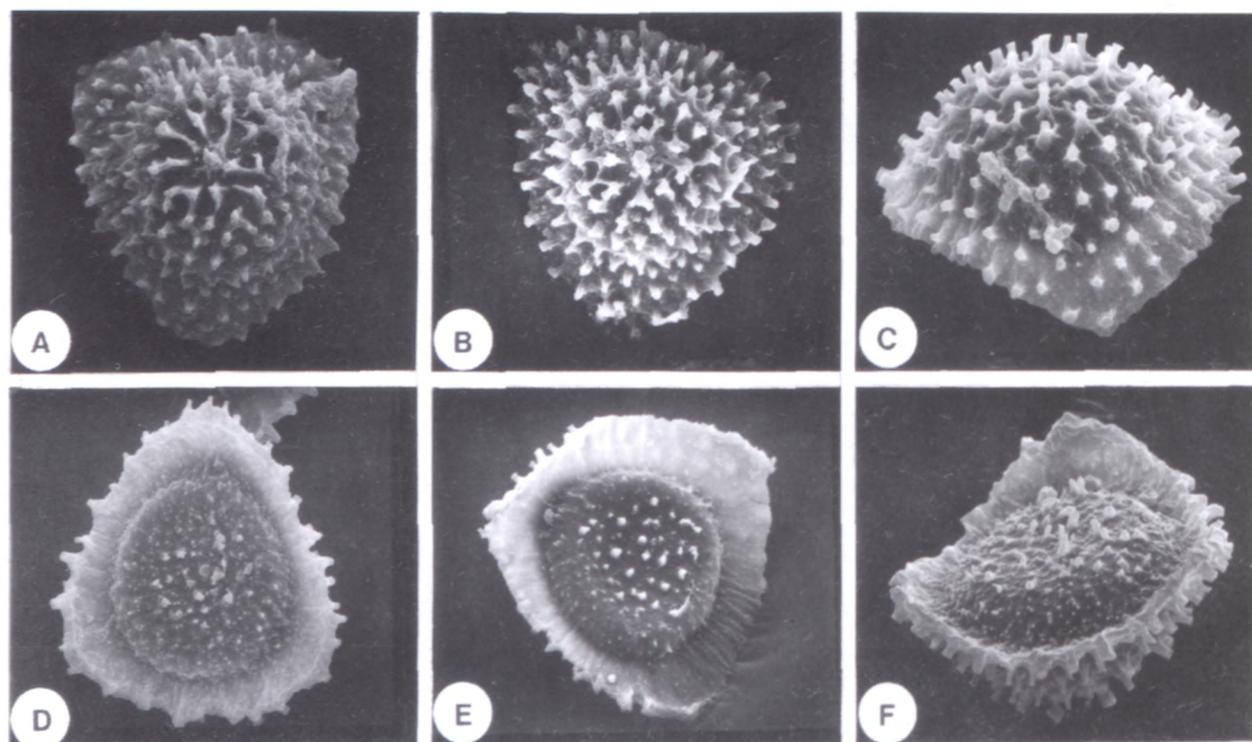


FIGURE 7.—*Riella alatospora*, E.L. Stephens BOL26400. SEM micrographs of spores. A, B, distal face; C, lateral view of part of distal face; D, E, proximal face with prominent wing; F, lateral view of proximal face, part of wing and some spines on distal face. A,  $\times 367$ ; B, D,  $\times 344$ ; C,  $\times 394$ ; E,  $\times 329$ ; F,  $\times 413$ .

$\mu\text{m}$  wide and 4-seriate, below only 50–55  $\mu\text{m}$  wide and uniseriate. *Foot* not bulbous, width nearly uniform along its length, 420–430  $\times$  220–240  $\mu\text{m}$ , in cross section surrounded by calyptra (Figure 5P). *Spores* 105–125  $\mu\text{m}$  diam., including prominent discoid wing,  $\pm$  20  $\mu\text{m}$  wide, increasing to  $\pm$  27.5  $\mu\text{m}$  wide at angles, golden brown,  $\pm$  triangular; distal face (Figure 7A–C) with  $\pm$  11 or 12 irregular rows of spines across diam., 5.0–7.5  $\mu\text{m}$  long, frequently dilated above, truncate, extending onto wing and  $\pm$  32 projecting beyond margin, 5.0–7.5  $\mu\text{m}$  between spines, central ones linked by basal connecting membranes forming indistinct reticulations; proximal face (Figure 7D–F) somewhat raised as centrally flattened dome, without triradiate mark, medianly with irregularly spaced papillae and marginally sprinkled with granules which extend onto wing, laterally surrounded by  $\pm$  concave wing, with radiating striations and marginally projecting spines.

#### DISCUSSION

Wigglesworth (1937) reports that there is a striking difference from the other *Riella* species in the appearance of the majority of cultured young plants of *R. alatospora* because they become heart-shaped at the top, instead of protruding at only one side as was usual in *R. purpureospora* Wigglesworth. I cannot comment on this, not having observed plants in culture.

In some of the specimens I examined, the marginal 5 or 6 rows of cells along the wing were without chloroplasts, which may perhaps be ascribed to the effects of partial drying.

In Wigglesworth (1937) there is a typographical error in the length of the plant as it is given in mm (3.5) instead of cm. She gives the size of the spores as  $\pm$  120  $\mu\text{m}$ , whereas Proskauer's (1955) measurements varied from 80 to 140  $\mu\text{m}$  and my own from 105 to 125  $\mu\text{m}$ .

*Riella alatospora* is easily distinguished by spores with a prominent discoid wing. Whether it has survived in ponds on the Cape Flats (Figure 4) is a matter of conjecture; at least it will not have been another victim of 'anonymous extinction' (Campbell 1989), thanks to the laudable efforts of the ladies Stephenson and Wigglesworth.

#### Specimens examined

*Stephens BOL26399–26401*; CC (= computer catalogue) 1627 (culture MANCH).

3. *Riella capensis* Cavers in Revue Bryologique 5: 81 (1903); Wigglesworth: 316 (1937); Prosk.: 68 (1955); S.W. Arnell: 7 (1963); Magill & Schelpe: 9 (1979). Type: cultivated from mud collected at shallow pond in neighbourhood of Port Elizabeth, leg. Hodgson in 1897 (MANCH 1630 = Manchester Museum, Owens College 22799, holo.!).

Plants erect, stems simple (Figure 8A, B), or irregularly pseudodichotomously branched, 10–30 mm tall, usually with V-shaped, twin, winged shoots at base from

common stem, then repeatedly, and reputedly becoming shrub-like with stalked, adventitious shoots, but not observed in scanty, remaining material. *Stem* slender, in cross section (Figure 8C) subround, slightly flattened dorsally and ventrally, 200–300  $\mu\text{m}$  or 8 cell rows thick, 300–350  $\mu\text{m}$  wide, outer cells smaller, almost isodiametric, 25–35  $\times$  27.5  $\mu\text{m}$ , inner cells mostly larger, rounded or angular, 25.0–37.5  $\times$  30.0–42.5  $\mu\text{m}$ . *Wing* unistratose, but often bistratose at join with stem, over-arching stem apex, where rounded and circinate, 1.5–2.8(–4.0) mm wide, narrowing below, but not disappearing, basally present, undulate; cells near stem 5- or 6-sided, 62.5–87.5  $\times$  25.0–32.5  $\mu\text{m}$ , near margin smaller, quadrate, 15.0–22.5  $\times$  12.5–22.5  $\mu\text{m}$ , scattered throughout wing, smaller cells filled with an oil body (Figure 8D). *Scales* dimorphic: lateral leaf scales crowded at apices of branches, further down sometimes paired, but mostly distant and alternate, rounded to obtusely triangular (Figure 8E–K), 430–750  $\times$  360–800  $\mu\text{m}$ , marginal cells  $\pm$  rectangular, 22.5–37.5  $\times$  27.5–47.5  $\mu\text{m}$ , occasionally smaller and filled with an oil body, cells in body of scale angular, 37.5–50.0  $\times$  32.5–42.5  $\mu\text{m}$ , those containing an oil body scattered about, 22.5–25.0  $\times$  32.5–37.5  $\mu\text{m}$ ; ventral scales smaller (Figure 8L, M), few, roughly triangular or rounded, 300–380  $\times$  310–330  $\mu\text{m}$ , marginal cells rectangular across, 20.0–32.5  $\times$  35–40  $\mu\text{m}$ , or in between, toward base,  $\pm$  50  $\times$  25  $\mu\text{m}$ , with smaller cells containing an oil body, cells in body of scale larger, 37.5–60.0  $\times$  27.5–35.0  $\mu\text{m}$ , with an occasional oil cell present,  $\pm$  25.0  $\times$  17.5  $\mu\text{m}$ .

Gemmae not seen.

Dioicous. Male plants absent in material studied, but described by Cavers (1903) as less branched (shrubby) and robust than female plants. *Involucres* (Figures 8N–P; 9F), up to 5, produced in acropetal sequence along same side of stem and only fairly rarely on the other side as well, 1875–2675  $\times$  1050–1350  $\mu\text{m}$ ,  $\pm$  smooth, ovoid-acuminate with gradual attenuation and then long drawn-out toward beak, mouth located apically on slender, finger-like projection,  $\pm$  200  $\times$  100  $\mu\text{m}$ , fringed with papillae, below also narrowed toward stalk, cells in involucre wall 5- or 6-sided, 32.5–50.0  $\times$  27.5–37.5  $\mu\text{m}$ , toward base somewhat longer. *Stalk* (Figure 8O) rarely almost absent, generally 500–625  $\times$  150–175  $\mu\text{m}$ , obliquely attached to stem where it widens (Figure 8N), mostly occupied by seta and foot, except for extreme base. *Calyptra* persistent, tristratose. *Capsule* globose, 750–825  $\mu\text{m}$  diam., occupying lower  $\frac{1}{3}$ – $\frac{1}{2}$  of involucre, wall (Figure 8Q) unistratose, yellow, cells 4–6-sided, 55–80  $\times$  45.0–82.5  $\mu\text{m}$ . *Seta* 275–350  $\mu\text{m}$  long, dark brown, expanded above and 4-seriate, narrow below, uniseriate. *Foot*  $\pm$  225  $\mu\text{m}$  long, yellowish, hardly bulbous, gradually widening from  $\pm$  100  $\mu\text{m}$  above to  $\pm$  225  $\mu\text{m}$  below. *Spores* 95–120  $\mu\text{m}$  diam., including spines, without wing, light brown,  $\pm$  triangular; distal face (Figure 9A, B) with 10–12 rows of spines across diam. and 30–36 projecting around margin, a few protruding from periphery of proximal face, though not excluded in the count, mostly broadly conical, tapering to an acute tip, but sometimes blunt, up to 10 or 12  $\mu\text{m}$  long, some basally connected by membranes not forming distinct reticulations, between spines lightly sprinkled

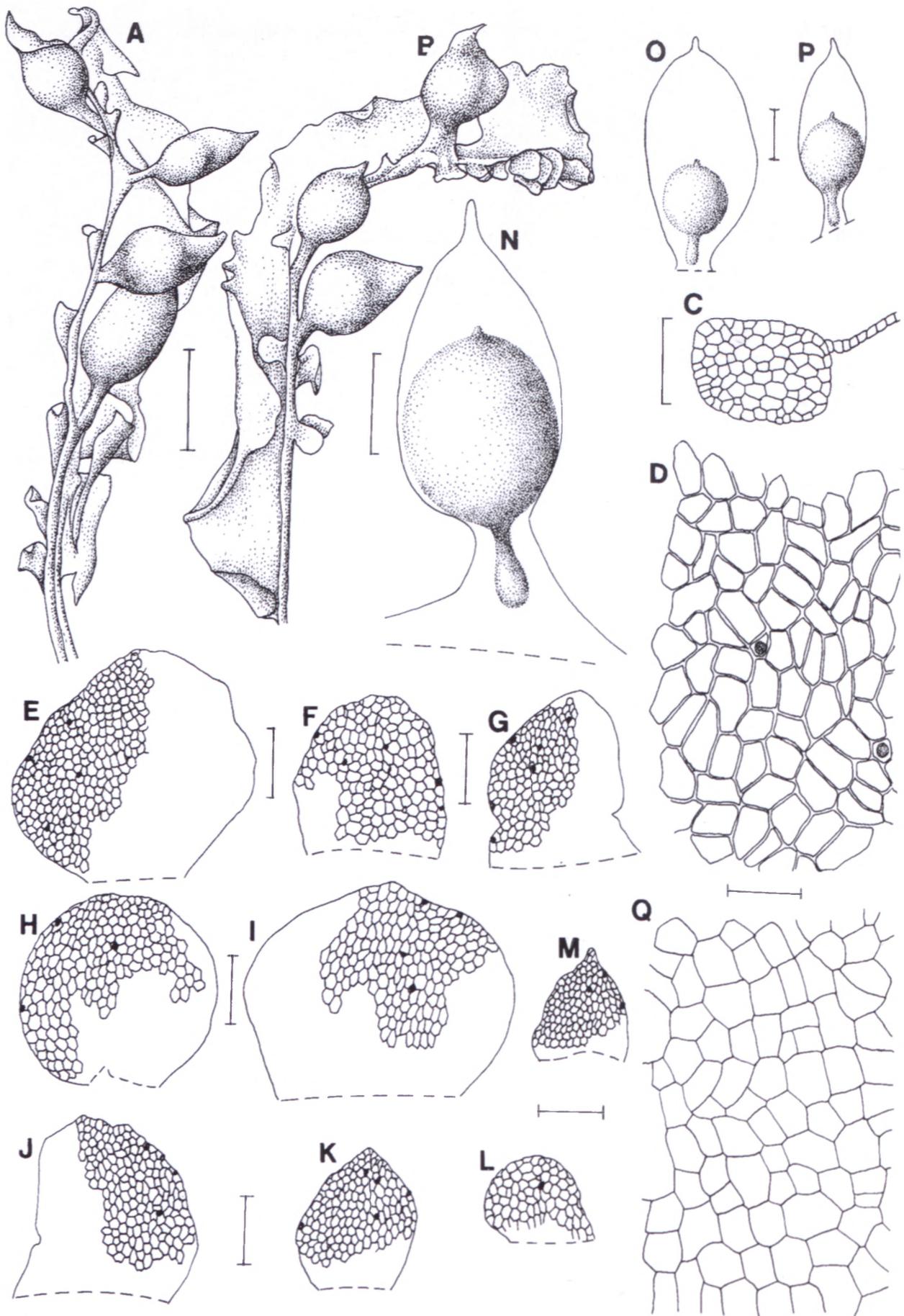


FIGURE 8.—*Riella capensis*, Hodgson MANCH1630. A, B, female plants with involucres mostly on same side of stem; C, c/s stem and part of wing; D, cells in wing, few smaller ones containing an oil body; E–K, lateral leaf scales; L, M, ventral leaf scales; N, P, involucre containing capsule, obliquely raised on stalk; O, involucre almost sessile; Q, cells in capsule wall. Scale bars: A, B, 2 mm; C, 200  $\mu$ m; D, 100  $\mu$ m; E–M, 250  $\mu$ m; N, O, P, 500  $\mu$ m; Q, 100  $\mu$ m.

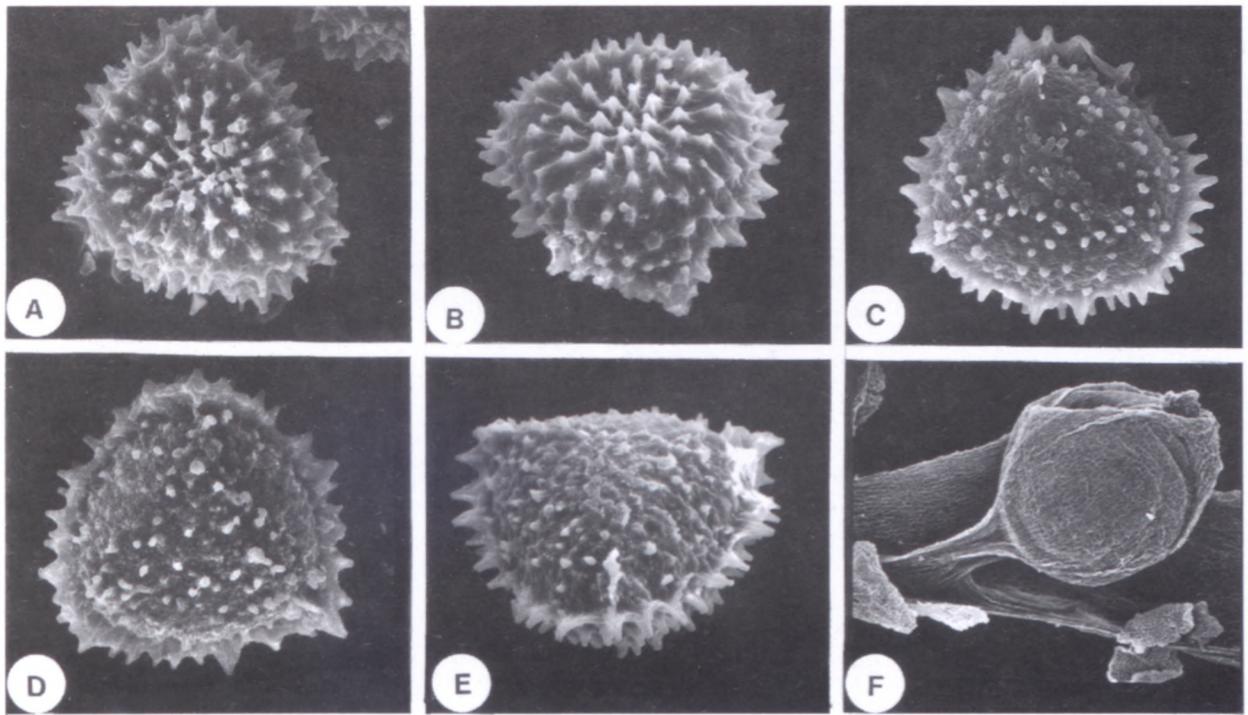


FIGURE 9.—*Riella capensis*, Hodgson MANCH1630. SEM micrographs of spores and involucre. A, distal face; B, distal face seen slightly from side; C, D, proximal face; E, proximal face partly from side, only two facets showing; F, apex of involucre collapsed, below obliquely raised on stalk, paired lateral leaf scales at stem. A,  $\times 352$ ; B,  $\times 367$ ; C,  $\times 382$ ; D,  $\times 394$ ; E,  $\times 375$ ; F,  $\times 25$ .

with some granules; proximal face (Figure 9C–E) slightly raised, not flat, marginal bases of spines joined by slightly striated webbing, from which individual, conical spines project outwards, triradiate mark faintly visible, papillae sparsely scattered over face, which is rather roughened with tiny, fairly indistinct granules.

#### DISCUSSION

Cavers did not give a Latin description of his new species, as it only became compulsory with the 1935 ICBN code (Briquet 1935); subsequently, Wigglesworth supplied a Latin description in 1937.

Cavers (1903) described the stem as circular in cross section, which probably would be more representative of the species than my section of it (Figure 8C). He also stated that he would describe the developmental stages of *R. capensis*, but I have not found a reference to such an article. He expressed the opinion that his new species came nearest to *R. helicophylla* Mont. from Spain, Algiers and Tunis.

Hassel de Menéndez, in her 1959 paper, points out the differences between *R. americana* and *R. capensis*, the latter much branched, the male plants with up to 100 (or more) antheridia, the female plants with up to 50 sporangia on a single plant, spore diam. 80  $\mu\text{m}$  and the spines 8  $\mu\text{m}$  long. Sim's (1926) record of it from Cape Town is evidently incorrect (Wigglesworth 1937).

Proskauer (1955) assigns a Pocock specimen collected on 12 December 1952 at the Palmiet River, Table Rock Farm, seven miles from Grahamstown on the Cradock Road, to *R. echinospora*, but then refers to the

marginal spines of the spores as showing light webbing, which, in my opinion, would place it nearer to *R. capensis*. I have seen no such webbing in *R. echinospora* spores, which are subround. His determination is therefore suspect.

Wigglesworth's (1937: fig. 7) illustration of the involucre of *R. capensis*, is rather less attenuate toward the beak, than those that I examined; her figure 9 of the proximal spore face, suggests some webbing at the base of the spines, whereas her figures 11 and 12 of *R. echinospora* spores clearly rule out the possibility of any webbing. Furthermore, she supposes that the course of growth in *R. capensis* plants followed the same lines as that of *R. alatospora*.

My visit to Port Elizabeth in October 1999 in an effort to find more material of *R. capensis* proved unsuccessful.

It was recently brought to my attention by Dr W.R. Harding, that Coetzer (1987) had reported *R. capensis* from Rocher Pan on the west coast. This collection has not been traced and the determination could not be verified.

#### Specimen examined

Hodgson MANCH1630 (22799).

4. *Riella echinospora* Wigglesworth in Journal of the Linnean Society of London, Botany 5: 321 (1937); Prosk.: 68 (1955); S.W.Arnell: 7 (1963); Magill & Schelpe: 9 (1979). Type: Orange Free State, Brandfort, salt pan, leg. Schonken (BOL!; MANCH!), presumed iso., from sticker on packet held in BOL.

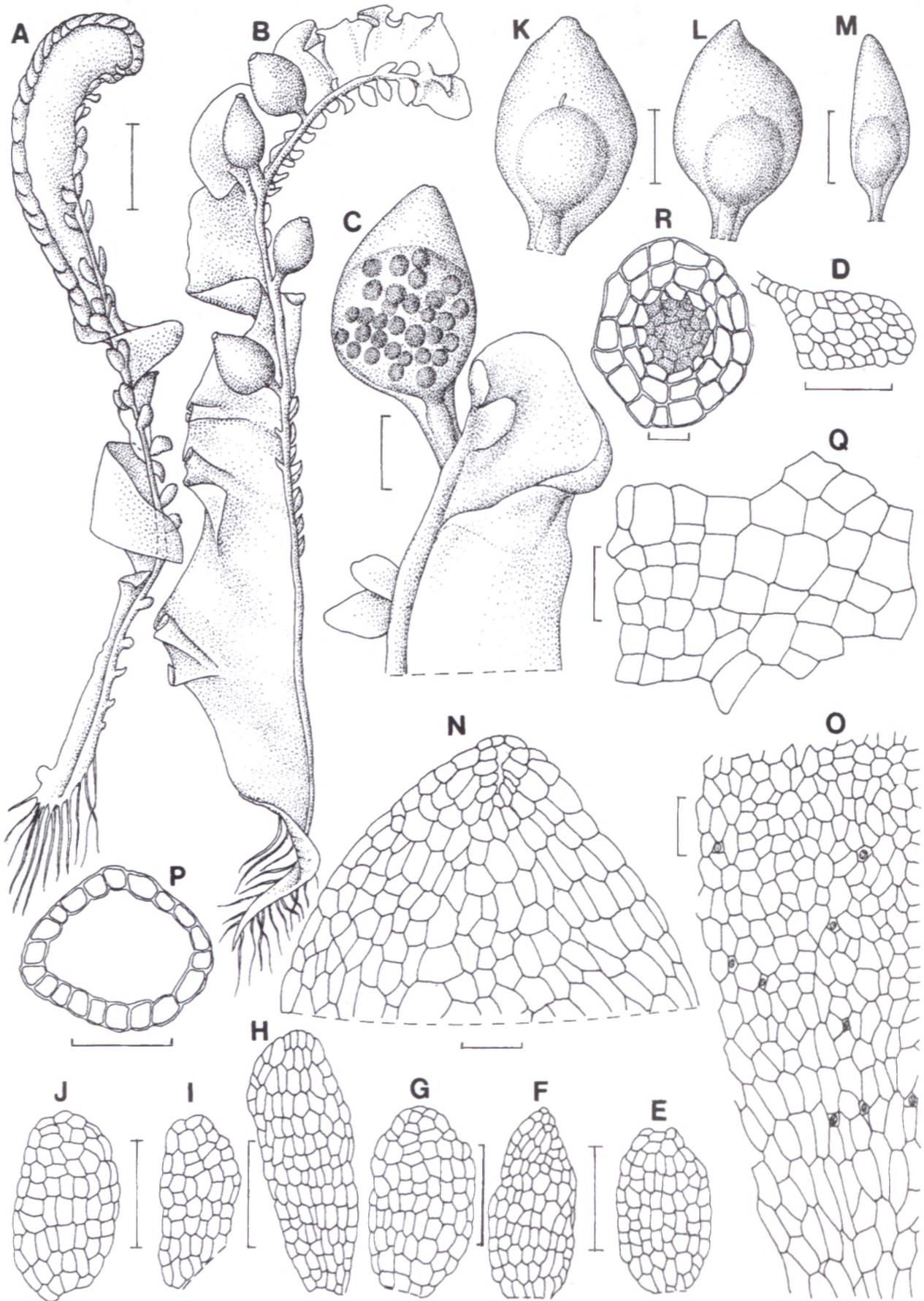


FIGURE 10.—*Riella echinospora*, Schonken BOL26029. A, male plant with row of antheridia along wing margin and numerous leaf scales along stem; B, female plant with several involucre; C, apical part of wing and involucre raised on stalk; D, c/s stem; E–H, lateral leaf scales; I, J, ventral leaf scales; K–M, involucres; N, detail of apical part of involucre with mouth occluded; O, cells in lower part of involucral wall; P, c/s involucral wall; Q, cells in capsule wall; R, c/s foot and 3-stratose calyptra. Scale bars: A, B, 2 mm; C, K–M, P, 500  $\mu$ m; D, 200  $\mu$ m; E–J, 250  $\mu$ m; N, O, Q, 100  $\mu$ m; R, 50  $\mu$ m.

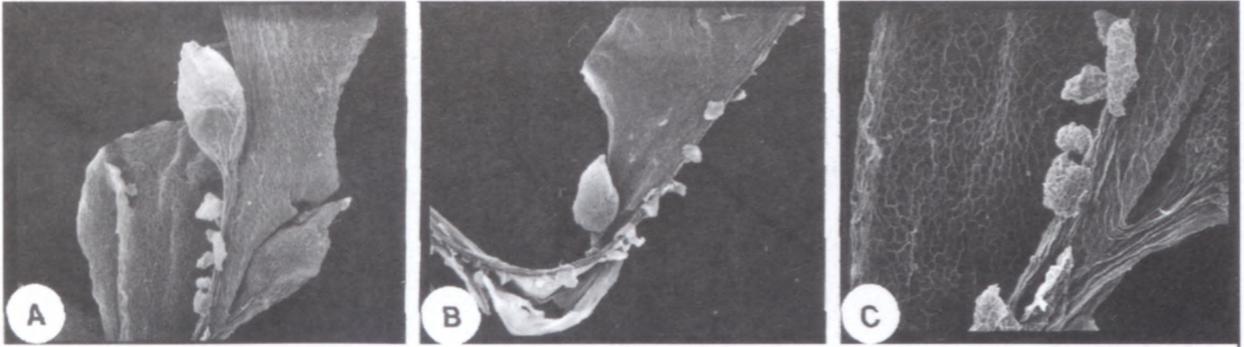


FIGURE 11.—*Riella echinospora*, Schonken BOL26029. SEM micrographs of plants. A, B, female plants with involucre and leaf scales; C, leaf scales along stem. A,  $\times 19$ ; B,  $\times 8$ ; C,  $\times 44$ .

Plants erect (Figure 10A, B), up to 35 mm tall; those developed from gemmae and remaining sterile, according to Wigglesworth (1937), branching freely and larger than fertile thalli. *Stem* (Figure 10D) slender, in cross section  $\pm$  ovoid, slightly flattened dorsally and ventrally, 150–225  $\mu\text{m}$  or  $\pm 6$  cell rows thick, 230–250  $\mu\text{m}$  wide, cells angular to rounded, 30.0–37.5  $\times$  25.0–42.5  $\mu\text{m}$ . *Wing* (Figure 10C) unistratose, 1.6–2.1 mm wide, highly undulate, narrowing below; cells near stem 5- or 6-sided, 85.0–137.5  $\times$  42.5–50.0  $\mu\text{m}$ , near margin smaller, 4- or 5-sided, 25.0–37.5  $\times$  17.5–25.0  $\mu\text{m}$ ; at margin, wedged between others, small cells, 12.5–17.5  $\times$  10–15  $\mu\text{m}$ , containing an oil body. *Scales* dimorphic: lateral leaf scales (Figures 10E–H; 11C) sometimes very numerous, crowded in pairs along stem, often associated with archegonia, oblong or tapering slightly toward apex, concave, attached to stem by row of cells, near tip with single mucilage cell, 400–510  $\times$  160–350  $\mu\text{m}$ , at margin cells quadrate or rectangular, 25.0–32.5  $\times$  25  $\mu\text{m}$ , small cells with oil bodies in between,  $\pm 12.5 \times 17.5 \mu\text{m}$ , inner

cells 4- or 5-sided, 30–35  $\times$  37.5–50.0  $\mu\text{m}$ , mostly larger below, 45–55  $\times$  30.0–42.5  $\mu\text{m}$ ; ventral leaf scales (Figure 10I, J) very similar to lateral leaf scales, but attached to stem by single cell.

Asexual reproduction by gemmae which are described as constricted in the middle (Wigglesworth 1937).

Dioicous. Male plants (Figure 10A) generally smaller than female plants. *Antheridia* in continuous series or interrupted, along wing margin. *Involucre* 4 or 5 in acropetal sequence along stem, ovoid, sometimes acuminate (Figures 10K–M; 11A, B),  $\pm$  smooth, 1375–1675  $\times$  950–1050  $\mu\text{m}$ , tapering above, mouth sometimes still occluded (Figure 10N), surrounded by smallish, apically rounded cells, 27.5–45.0  $\times$  15.0–22.5  $\mu\text{m}$ , below contracted toward stalk, in cross section  $\pm$  ovoid (Figure 10P), cells in involucre wall (Figure 10O) 4–6-sided, 40–75  $\times$  25–40  $\mu\text{m}$ , larger toward base, 87.5–147.5  $\times$  27.5–42.5  $\mu\text{m}$ . *Stalk*  $\pm 375 \times 270 \mu\text{m}$ , obliquely attached

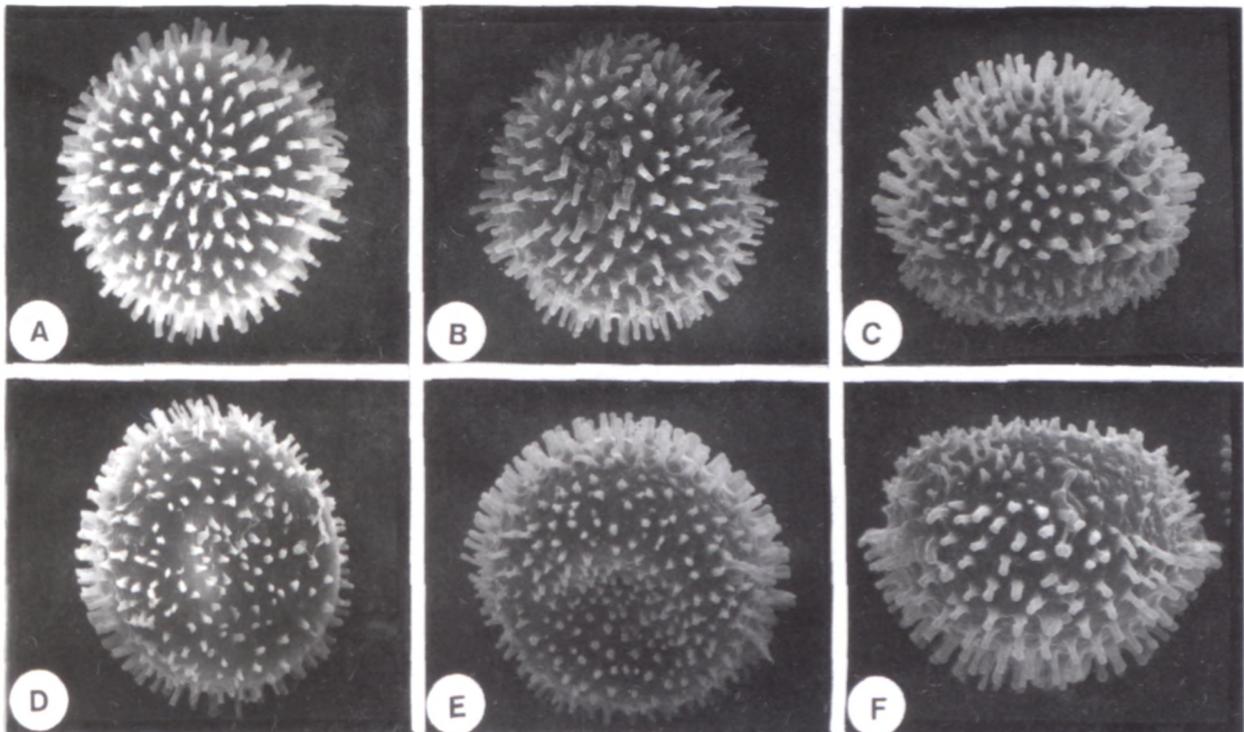


FIGURE 12.—*Riella echinospora*, Schonken BOL26029. SEM micrographs of spores. A, B, distal face; C, lateral view of part of distal face above and proximal face below; D, E, proximal face; F, lateral view of part of proximal face above and distal face below. A,  $\times 417$ ; B,  $\times 455$ ; C,  $\times 531$ ; D,  $\times 409$ ; E,  $\times 394$ ; F,  $\times 489$ .

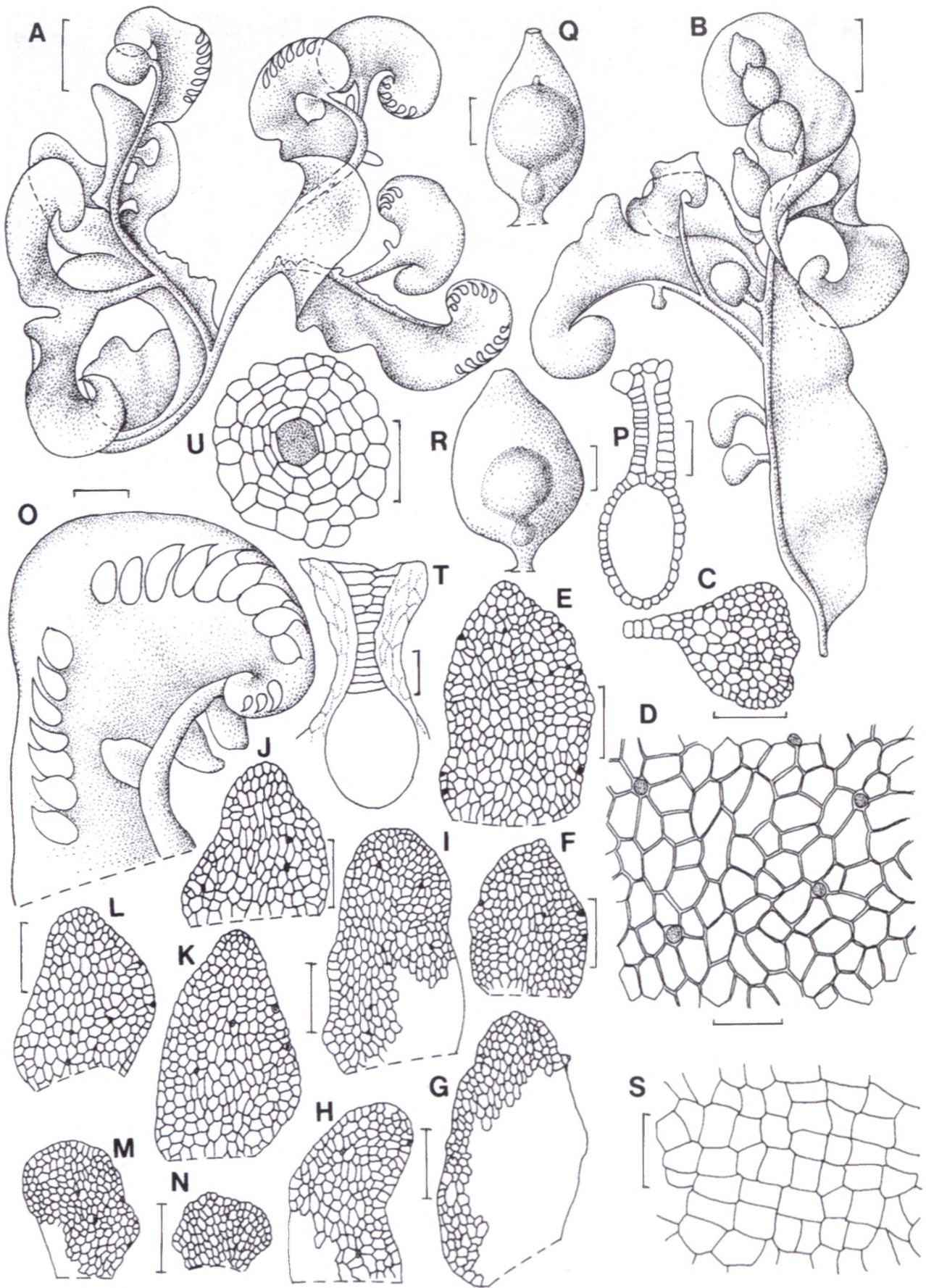


FIGURE 13.—*Riella purpureospora*, Harding CH13724 (PRE). A, furcate male plant; B, female plant with involucre near apex; C, c/s stem and part of wing; D, dimorphic cells in wing with numerous chloroplasts, scattered smaller cells with oil body in each; E–L, lateral leaf scales; M, N, ventral leaf scales; O, apical part of male plant with interrupted row of antheridia, proximal ones discharged; P, archegonium; Q, R, involucre; S, capsule wall; T, surface view of seta and foot; U, c/s calyptra surrounding seta. Scale bars: A, B, 2 mm; C, 200 µm; D, S, T, 100 µm; E–N, 250 µm; O, 500 µm; P, U, 50 µm; Q, R, 500 µm.

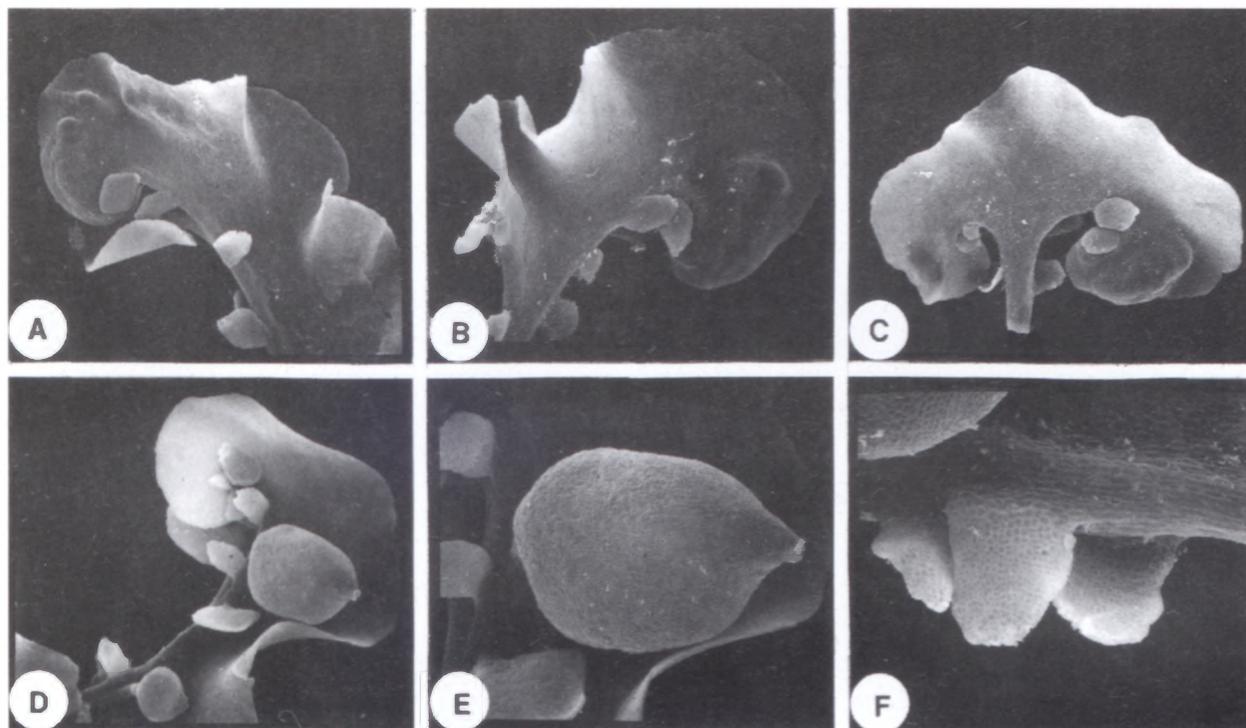


FIGURE 14.—*Riella purpureospora*, Harding CH13724 (PRE). SEM micrographs of plants. A, B, apical part of male plant with antheridia near margin and leaf scales along stem; C, pseudodichotomous branching in male plant; D, female plant with 3 involucre and leaf scales along stem; E, more enlarged lateral view of involucre; F, small part of stem with leaf scales. A,  $\times 9.6$ ; B,  $\times 15.7$ ; C,  $\times 8.8$ ; D,  $\times 8.4$ ; E,  $\times 18.4$ ; F,  $\times 34.8$ .

to stem, occupied by seta and foot. *Calyptra* mostly bistratose. *Capsule* occupying lower  $\pm \frac{3}{4}$  of involucre, subglobose, 775–850  $\mu\text{m}$  diam., wall pale yellow, cells irregular in shape and size (Figure 10Q), 30–90  $\times$  40.0–52.5  $\mu\text{m}$ . *Seta*  $\pm 100$   $\mu\text{m}$  long, dark red, not expanded above. *Foot*  $\pm 250$   $\mu\text{m}$  long, width  $\pm$  uniform throughout its length, in cross section (Figure 10R), surrounded by calyptra and up to 300  $\mu\text{m}$  wide. *Spores* 87.5–97.5  $\mu\text{m}$  diam., including spines, without wing, light brown, subglobose; distal face (Figure 12A–C, F) fairly densely covered with 13–16 irregular rows of spines across diam., 50 or more projecting around periphery, but rather difficult to count as several rows involved due to roundness of spore, mostly slender and acute, occasionally apically truncate and slightly swollen or dilated at tips, up to 10  $\mu\text{m}$  long, not basally connected,  $\pm 5$   $\mu\text{m}$  between spines; proximal face (Figure 12D–F) raised, often indented in the centre, covered with  $\pm 19$  rows of smaller and finer spines across, up to 4 or 5  $\mu\text{m}$  long, in between with some papillae, triradiate mark absent.

#### DISCUSSION

It is possible that *Riella echinospora* is more widespread than just the Brandfort area, as Arnell (1957, 1963) also recorded it from a Volk collection in Namibia at Haribes, Marienthal, 'In seichthem Wasser auf feinem Sand, häufig'. Proskauer (1955) also reported that 'a sporeling with attached spore probably belonging to this species was isolated during class work at Berkeley from a culture prepared from soil gathered by Dr Pocock on the Cape Flats'. Regarding his reference to the specimen from 'the Palmiet River, Table Rock Farm', I have already commented on its spores in my discussion of *R. capensis*.

In October 1999 on my way through the Free State to the Eastern Cape, it was noticed that there were numerous pans visible from the highway. It would be worth investigating them for the presence of *Riella* plants.

#### Specimens examined

Schonken BOL26029; CC (= computer catalogue) 1632–1635; 1637–1640; 1642–1649 (cultures MANCH).

5. *Riella purpureospora* Wigglesworth in Journal of the Linnean Society of London, Botany 5: 312 (1937); Prosk.: 66 (1955); S.W.Arnell: 7 (1963); Magill & Schelpe: 9 (1979). Type: prope Cape Town, legit E.L. Stephens, atque usu sporarum illae originis coluit G. Wigglesworth (BOL!, MANCH!) (? type not designated).

Plants erect, 20–60 mm tall, stems sparsely to frequently furcate, some branches again furcate, occasionally with several pseudodichotomies close together, the daughter stems growing new wings; stalked adventitious shoots formed anywhere along parent stem (Figures 13A, B; 14C). *Stem* in cross section (Figure 13C) subround, 330–350  $\mu\text{m}$  or 10 cell rows thick, 350–380  $\mu\text{m}$  wide, outer cells isodiametric, 25.0–37.5  $\times$  20.0–32.5  $\mu\text{m}$ , inner cells angular, mostly larger, 30–60  $\times$  30–40  $\mu\text{m}$ . *Wing* unistratose, but bistratose at join with stem, overarching stem apex, 1.3–2.75  $\mu\text{m}$  wide, undulate, narrowing below and then disappearing altogether, leaving basal part of stem wingless; cells near stem 5- or 6-sided, 50.0–87.5  $\times$  30–50  $\mu\text{m}$ , near margin smaller, 4- or 5-sided, 20.0–32.5  $\times$  15–20  $\mu\text{m}$ ; scattered throughout wing, numerous small cells filled with an oil body (Figure 13D). *Scales* dimorphic (Figure 14F): lateral leaf scales (Figure 13E–L) at irregular intervals,

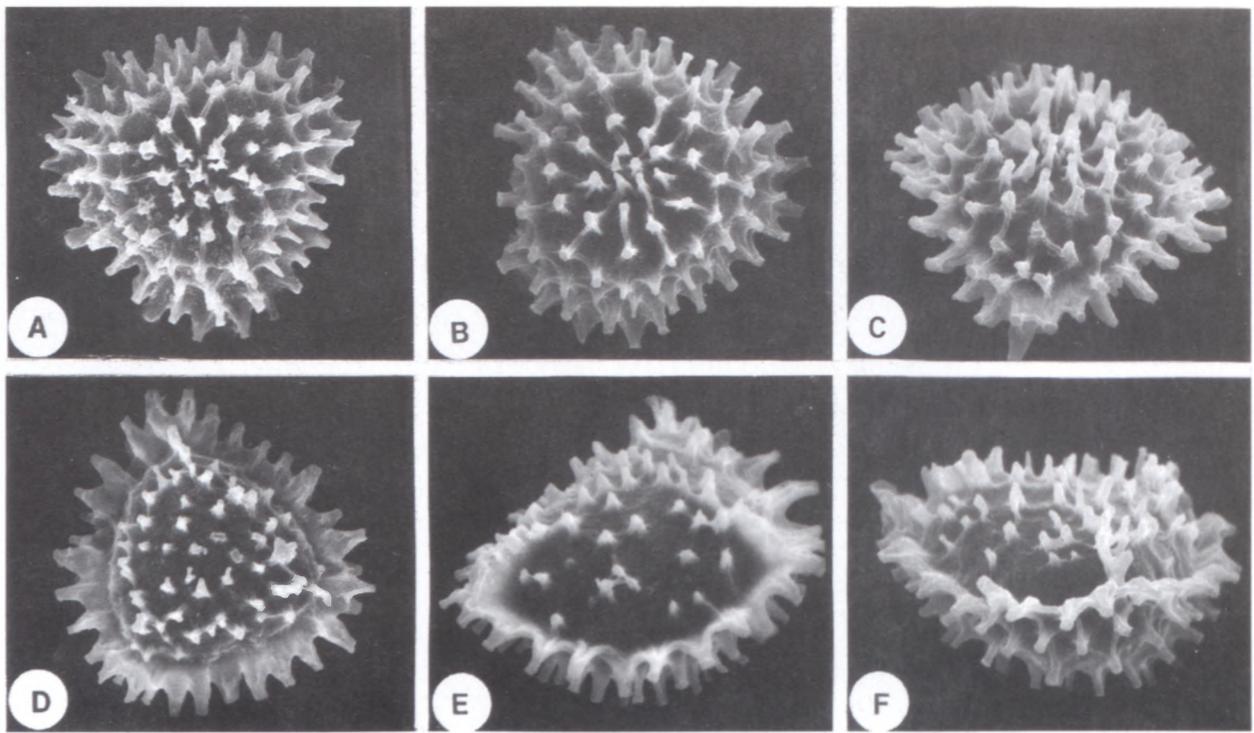


FIGURE 15.—*Riella purpureospora*, Garside 6656 (BOL). SEM micrographs of spores. A, B, distal face; C, part of distal face; D, proximal face, showing webbing at base of spines; E, one facet of proximal face; F, lateral view of proximal face, part of wing and some spines on distal face. A,  $\times 340$ ; B,  $\times 455$ ; C,  $\times 382$ ; D,  $\times 344$ ; E,  $\times 524$ ; F,  $\times 554$ .

obliquely or vertically attached on both sides of stem, often in pairs, oblong, lingulate or tapering apically, 570–925  $\times$  310–800  $\mu\text{m}$ , unistratose, marginal cells mostly 4-sided, 15–30  $\times$  20.0–37.5  $\mu\text{m}$ , with smaller cells,  $\pm 20.0 \times 17.5 \mu\text{m}$ , containing an oil body, wedged in between, cells in body of scale 4–6-sided, 25.0–57.5  $\times$  20.0–52.5  $\mu\text{m}$ , scattered about in between, smaller cells  $\pm 25 \times 25 \mu\text{m}$ , each with an oil body; ventral leaf scales (Figure 13M, N) fewer and rather smaller, irregularly shaped or bluntly triangular, 270–450  $\times$  320–480  $\mu\text{m}$ , marginal cells rectangular or  $\pm$  isodiametric, 25.0–37.5  $\times$  17.5–32.5  $\mu\text{m}$ , with smaller cells containing an oil body wedged in between, cells in scale body 4–6-sided, 25–45  $\times$  25–30  $\mu\text{m}$ , and in between an occasional smaller cell with an oil body.

Dioicous. Male plants somewhat smaller than female plants. *Antheridia* numerous, in a single, linear series (Figure 14A, B), in pockets of up to 23, in acroscopic sequence along wing margin, but sometimes interrupted (Figure 13O), ovoid, 350  $\times$  250–270  $\mu\text{m}$ , discharging through individual ducts, mostly sloping toward and opening by pores at edge of wing; cells in wing covering antheridia rather larger than those at periphery of antheridia. *Archegonia* (Figure 13P) at maturity with 4 cover cells at apex of neck, these swollen and separating from each other, leaving neck open for entrance of antherozoids. *Involucre*s (Figures 13Q, R; 14D, E) up to 7 produced in acropetal sequence along stem, pyriform,  $\pm$  smooth, 2375–2575  $\mu\text{m}$  long,  $\pm 1600 \mu\text{m}$  wide across widest part, abruptly narrowing to beak,  $\pm 200 \mu\text{m}$  wide and surrounded by  $\pm 12$  cells in an irregularly protruding row, below also contracted toward stalk, cells in involucre wall 5- or 6-sided, 40–60  $\times$  32.5–45.0  $\mu\text{m}$ . *Stalk*  $\pm 375 \times 250 \mu\text{m}$ , obliquely attached to stem, upper  $\pm 125 \mu\text{m}$  occupied by basal part of foot. *Calyptra* multistratose,

in cross section up to 4 layers of cells surrounding inner haustorial cells of foot (Figure 13U). *Capsule* globose, up to 1200  $\mu\text{m}$  diam. at maturity, wall red or mauve, unistratose, cells (Figure 13S) 4- or 5-sided, 42.5–70.0  $\times$  30.0–47.5  $\mu\text{m}$ . *Seta* (Figure 13T)  $\pm 210 \mu\text{m}$  long, dark red, upper  $\pm 100 \mu\text{m}$  expanded, funnel-shaped, narrow below, only  $\pm 35 \mu\text{m}$  wide, uniseriate. *Foot* (Figure 13T)  $\pm 260 \mu\text{m}$  long, gradually expanding from narrow upper part to  $\pm 200 \mu\text{m}$  wide below. *Spores* 82.5–117.5  $\mu\text{m}$  diam., including spines, without wing, purple or red,  $\pm$  triangular; distal face (Figure 15A–C), with  $\pm 12$  rows of spines across diam. and 25–30 projecting around margin, mostly stout and truncate, rarely acute, 7.5–10.0  $\mu\text{m}$  long, 5–10  $\mu\text{m}$  between spines, basally connected by membranes forming irregular reticulations; proximal face (Figure 15D–F) raised, not flat, marginally with basally webbed spines, sometimes webbing very prominent, appearing almost wing-like, 7.5–12.5  $\mu\text{m}$  wide, with spines projecting outwards from it, triradiate mark occasionally nearly complete, but mostly only present toward angles, rest of face irregularly dotted with up to 15 low spines per facet.

#### DISCUSSION

So far, *R. purpureospora* is the only species to have been collected in recent times, viz. by Dr W.R. Harding. It is quite a robust plant and is probably the easiest species to identify because of its purple or red spores and capsule wall, as well as the pronounced webbing between the bases of the marginal spines on the proximal spore face.

The reference to the separation of the four cover cells of the archegonial neck in my description is from Thompson (1942) who referred to *R. affinis*, but it is equally applicable to other species, i.e. *R. purpureospora*.

The Harding specimen was collected at Blouvillei, Cape Town vicinity (Figure 4), in an ephemeral pan which contains water between April and September, together with *Pseudaltheia aschersoniana* and *Bolboschoenus maritimus*. The pH of the water was 9.6, the alkalinity (as CaCO<sub>3</sub>) 246 mg per litre and the salinity (as Na) 3813 mg per litre (W.R. Harding pers. comm.).

#### Specimens examined

Garside 6656 (BOL); Harding CH13724 (PRE); Stephens CC (= computer catalogue) 1613–1626, 1631, 1636 (cultures MANCH); Walgate 999 (BOL).

*Riella* sp.—from Valkenberg vlei, Wigglesworth, in *Journal of the Linnean Society of London, Botany* 5: 324 (1937); Prosk.: 68 (1955). Cape Town, Valkenberg Vlei, legit E.L. Stephens BOL26031!

This species has not been treated in this study, as there are no ripe spores in the original collection and it has not been collected again. As mentioned in the introduction, the spore ornamentation is essential for correct identification of *Riella* species.

#### ECOLOGY

The five *Riella* species known from southern Africa, are from widely scattered localities, ranging from the summer rainfall area of central Free State (*R. echinospora*), to the winter rainfall areas of the Cape Flats (*R. alatospora* and *R. purpureospora*), in Western Cape, and extending to parts of Eastern Cape (*R. affinis* and *R. capensis*), which receive sparse summer and winter rains. The vegetation types in these localities, according to Low & Rebelo (1996), are the following: central Free State: Dry Sandy Highveld Grassland; Western Cape, Cape Flats: Sandplain Fynbos; Eastern Cape, Port Elizabeth area: Mesic Succulent Thicket; north of Grahamstown: Eastern Mixed Nama Karoo.

*Riella* species grow in temporary or permanent pools, vleis or intermittent streams, containing fresh or brackish water. Hässel de Menéndez (1987) on the other hand, found that Argentinian *Riella* species did not grow in temporary dry ponds, but rather in lakes, some of which are artificial. *Riella* thalli cannot, however, withstand desiccation, even for a short while.

It is thought that *Riella* spores may be transported by wind or by birds (Hässel de Menéndez 1987). Schuster (1992) is of the opinion that it is unlikely, although theoretically possible, that thalli (and spores) may be disseminated on the feet of wading birds from one site to the next. Apparently spores can pass through their gut unharmed and may be transported in this way over distances limited to under 80–100 km.

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