LUNULARIACEAE

FRUITING LUNULARIA CRUCIATA, NOW ALSO REPORTED FROM SOUTHERN AFRICA

Sexual reproduction in Lunularia cruciata (L.) Dumort. ex Lindb. occurs only rarely or sporadically. In an earlier article on Lunularia cruciata (Perold 1993), I did not describe mature archegoniophores with sporophytes, because no examples were available at PRE for study. In an attempt to raise them in cultivation, male plants collected in a nursery in Krugersdorp, west of Johannesburg (Koekemoer 1004) and female plants from Harold Porter National Botanical Garden, Betty's Bay (Perold et al. 3029), were planted together in September 1993 on soil in a pot and kept in a secluded courtyard. Although growing well and watered regularly, fertilization did not take place.

Recently, in late spring, on 8 November 1994, I received live material with androecial discs (Figure 5A) and archegoniophores in various stages of maturity (Figures 5B. C) from Mrs Susan Strauss, who maintains a shadenet enclosure. Although not new to science, another description of mature archegoniophores and sporophytes, this time from southern Africa, was deemed permissible, as Arnell's (1963) description, in which he mistakenly refers to the "peduncle of the female organ" as furrowed, is very brief and is almost certainly not based on southern African material. Even Saxton (1931), who described the life history of Lunularia cruciata partly from southern African collections, had to wait many years, i.e. from 1908, 240



FIGURE 5.—*Lunularia cruciata*. A, thalli with androecial discs; B, thalli with young, still sessile archegoniophores; C, stalked archegoniophores; D, mature archegoniophore, shedding spores and elaters; E, portion of stalk in transverse section, showing cortical and medullary cells; F, seta in transverse section; G, germinating spore. A–G, S. Strauss 64. A, B, × 2.5; C, × 2; D, × 3: E, × 175; F, × 70; G, × 700. E–G, LM photographs.

when initially 'a small patch of fertile plants was found ... in the Municipal Gardens at Cape Town' [which he appears not to have described], until fruiting material was eventually forwarded to him from Dartmouth, England, in 1925–1928. The youngest stages of the archegoniophores were missing, however, and their description was only completed more than 20 years later, by Benson-Evans & Hughes (1954), based on English collections. Campbell

(1965) also added some supplementary notes regarding the early stages in New Zealand material. Schuster (1992) reports the species as relatively often fertile in the south of Spain, but rarely in North America. Sérgio & Viana (1973) found one-fifth of the collections in Portugal to have sporophytes. Germination of the spores (Figure 5G) was described by Groenland (1954), Chalaud (1932) and also by Campbell (1965) but, as far as I am aware, SEM

Bothalia 25,2 (1995)

micrographs of the spores and elaters have not previously been published.

DESCRIPTION OF ARCHEGONIOPHORE, SPOROPHYTES AND SPORES

Juvenile archegoniophore sessile (Figure 5B), apical part roundly convex to shortly 4-lobed, ± 2 mm in diameter, with small, central swelling, lime-green and somewhat shiny, basally surrounded by densely imbricate layers of cottony, white scales with upper edges irregularly fringed with filiform cellular appendages (Figure 6F). Archegonia in 4 groups, up to 8 (or more) in each, of these only 1 or 2(3)or even none becoming fertilized, located between lobes, opposite indentations, and surrounded by furrows, with raised margins which rapidly grow out to form tubular involucres. By expansion of central domed region, all subsequently carried to underside, initially drooping, later almost horizontally spreading outwards in shape of a cross, from a common, reduced central disc lacking photosynthetic tissue. Involucres yellowish white, almost smooth, rather delicate, 5 cell layers (\pm 160 µm) thick, numerous oil bodies present, outer cells $35.0-75.0 \times 25.0-37.5 \,\mu\text{m}$, 4- or 5-sided, some long-rectangular; smaller, however, $25-30 \times 25-35$ µm, at margins of eventual distal opening, through which, by elongation of setae, capsules become exserted (Figure 5D), after rupturing calyptra; pseudoperianth lacking. When sporophytes nearly ripe, stalk elongates, trailing silvery white, thread-like filaments with it, archegoniophore still partially covered by scales, and foot of stalk surrounded by large, erect scales, up to $2500 \times 2500 \mu m$, cells 4-6(-7)-sided, $37.5-52.5 \times 22.5-25.0 \ \mu\text{m}$, filiform appendages consisting of elongated cells, $\pm 65 \times 20 \mu m$, linearly arranged in a single row. Stalk eventually up to 34 mm long, gradually narrowing upwards, translucent white, in transverse section

rounded to oval toward base, 825-950 × 750-850 µm, cortical cells in 1 row, $15.0-22.5 \times 12.5-25.0 \mu m$, outer walls hardly thicker, medullary cells angular, 35.0-47.5 µm wide (Figure 5E), slightly thickened at corners, lacking rhizoid furrow as well as photosynthetic tissue, shaggy with scattered, white, thread-like filaments; after spores and elaters have been shed, soon collapsing. Calyptra enlarging with growth of sporophyte, its wall ± 4 cell layers (62.5 µm) thick, outer cells rectangular or polygonal, 45-60 × 20-25 µm, archegonial neck remaining attached. Sporophyte with foot subspherical, small, green; seta hyaline, 150-300 μ m in diameter, rapidly elongating to ± 2 mm, in transverse section (Figure 5F), cortical cells 30.0-32.5 × 17.5-25.0 µm, medullary cells round or isodiametric, 25-40 µm wide, walls slightly undulate; capsule dark brown, obovoid, ± 1.25 mm long, wall unistratose, lacking thickenings, cells rectangular, 20.0-25.0 × 12.5-15.0 µm and 25 µm thick, tiny distal cap bistratose and soon shed intact, dehiscing lengthwise into 4 lanceolate valves, some bifid at apex, folding back to base of capsule and releasing numerous spores and elaters. Spores light brown, when fresh many filled with chloroplasts, apolar, triradiate mark absent (Figure 6A), mostly spherical or ovate (Figure 6B), frequently with indentations (Figure 6C), wall thin, densely granulate (Figure 6D), diameter (12.5-)15.0-22.5 µm; enlarging and germinating after 3 or 4 weeks (Figure 6G), a colourless germ rhizoid (Nehira 1983) emerging from it. Elaters light brown, bispiral (Figure 6E), longly tapering at both ends, 320-350 µm long, 5-6 µm wide in centre, tips 2.5 µm.

DISCUSSION

Various reasons have been suggested for the low incidence of sexual reproduction in *Lunularia cruciata* but no causal relationship could be found between its sexual fer-



FIGURE 6.-Lunularia cruciata. A, round spore; B, ovate spore; C, indented spore; D, granular ornamentation on exine much enlarged; E, part of 2 elaters; F, young archegoniophore, covered with scales with long filiform appendages at margins. A, B, D, E, S. Strauss 64; C, Angusto LISU 147800; F, Koekemoer 1004. A, × 226; B, × 199; C, × 222; D, × 612; E, × 191; F, × 31. A–F, SEM micrographs.

tility or sterility and, for example, the presence or absence of the fungus, Phoma lunulariicola Ramsay, often associated with it (Benson-Evans & Hughes 1954). Unusual weather conditions were shown by Goodman (1956) to have no obvious correlation with the initiation of receptacles. On the other hand, Benson-Evans & Hughes (1954) found that there was an obvious correlation between the regular production of sexual organs and a Mediterranean type of climate. They also conclude that there is a preceding low temperature requirement in Lunularia and that this is comparable to vernalization in higher plants. Campbell (1965) refers to the work by Nachmony-Bascomb & Schwabe (1963) who demonstrated a response to photoperiod in Israeli plants. However, any interpretation of the behaviour of the New Zealand plants in the light of these findings was complicated by the fact that winter temperatures in New Zealand are much lower than those in Israel. Sérgio & Viana (1973) suggest 'that the availability of water is the limiting factor in the development of the sporophytes as it was shown by the geographic distribution of the fruiting plants'; and they continue: 'this distribution is correlated with a humid Mediterranean type of climate^{*}.

As far as the southern African plants are concerned, it is possible that the formation of gametangiophores was initiated by the unusually severe winter we experienced in 1994. Although the plants were somewhat protected in Mrs Strauss' shade-net enclosure, it was unheated and they may have become 'vernalized'. Synchronous maturation of spermatozoids and eggs and their close proximity must have led to fertilization and the subsequent production of sporophytes several months later. phytes. My thanks also to Dr C. Sérgio, Lisbon, for sending me material with mature archegoniophores from Portugal and for reviewing this note; to Mrs A. Romanowski for taking some of the photographs and for printing all of them, also to Mrs J. Mulvenna for typing the manuscript.

REFERENCES

- ARNELL, S.W. 1963. *Hepaticae of South Africa*. Swedish Natural Science Council, Stockholm.
- BENSON-EVANS, K. & HUGHES, J.G. 1954. The physiology of sexual reproduction in *Lunularia cruciata* (L.) Dumort. *Transactions of* the British Bryological Society 2: 513–521.
- CAMPBELL, E.O 1965. Lunularia in New Zealand. Tuatara 113: 31-42.
- CHALAUD, G. 1932. Germination des spores et phase protonémique. Manual of Bryology: 89–108.
- GOODMAN, G.T. 1956. Sexual Lunularia cruciata (L.) Dumort. in South Wales. Transactions of the British Bryological Society 3: 98–102.
- GROENLAND, J. 1854. Mémoire sur la germination de quelques Hépatiques. Annales des sciences naturelles, Sér. 4: 5–29.
- NACHMONY-BASCOMB, S. & SCHWABE, W.W. 1963. Growth and dormancy in *Lunularia cruciata* (L.) Dumort. 1. *Journal of Experimental Botany* 14: 153–171.
- NEHIRA, K. 1983. Spore germination, protonema development and sporeling development. *New Manual of Bryology* 1: 343–385.
- PEROLD, S.M. 1993. Studies in the Marchantiales (Hepaticae) from southern Africa. 1. The genus *Dumortiera* and *D. hirsuta*; the genus *Lunularia* and *L. cruciata*. *Bothalia* 23: 49–57.
- SAXTON, W.T. 1931. The life history of *Lunularia cruciata* (L.) Dumort., with special reference to the archegoniophore and sporophyte. *Transactions of the Royal Society of South Africa* 19: 259–268.
- SÉRGIO, C. & VIANA, M.J. 1973. Sur la fertilité de Lunularia cruciata (L.) Dum. au Portugal. Revista da Faculdade de Ciências de Lisboa 17: 703–720.
- SCHUSTER, R.M. 1992. The hepaticae and anthocerotae of North America 6: 1–937.

ACKNOWLEDGEMENTS

I sincerely wish to thank Mrs Susan Strauss of Pretoria for bringing me plants of *Lunularia cruciata* with sporoS.M. PEROLD*

^{*}National Botanical Institute, Private Bag X101, Pretoria (0001, MS. received; 1995-01-17.