

Sporocarpic Species of Endogonaceae in Australia

P. A. Tandy

Plant Pathology Department, Waite Agricultural Research Institute,
University of Adelaide, Glen Osmond, S.A. 5064; present address:
Municipal Offices, P.O. Box 197, Werribee, Vic. 3030.

Abstract

Fructifications of nine Australian members of the Endogonaceae are described. Five of these are new species: *Endogone aggregata*, *E. reticulata*, *E. crassa*, *Glomus tubaeformis*, and *Glomus tener*. *Endogone flammicorona* Trappe & Gerdemann is reported for the first time in the southern hemisphere, and *Glomus macrocarpus* Tul. & Tul. var. *macrocarpus* is a new record for South Australia. A key to the known sporocarpic species of the Endogonaceae in Australia is provided.

Introduction

There are few references to the collection or description of fructifications of the Endogonaceae in Australia. There are published accounts of only two species: *Endogone australis* Berk. from Tasmania (Berkeley 1860; syn. *Glomus macrocarpus* Tul. & Tul. var. *macrocarpus*, fide Gerdemann and Trappe 1974), and *E. tuberculosa* Lloyd from New South Wales (Lloyd 1918; Cleland and Cheel 1918; Thaxter 1922; Gerdemann and Trappe 1974). Three species collected in Tasmania have been examined by Trappe: *Glomus macrocarpus* var. *macrocarpus*, *G. microcarpus* Tul. & Tul. and *G. pulvinatus* (P. Henn.) Trappe & Gerdemann. Apart from this, there are no records or specimens of sporocarpic Endogonaceae in any of the major Australian mycological collections. While spores of *Endogone* and *Glomus* species have frequently been isolated from Australian soils (Warcup 1957; Mosse and Bowen 1968*a*, 1968*b*; Tandy 1969; Bevege 1971; Bevege and Richards 1971) most of these occurred singly or formed only rudimentary sporocarps. Such non-sporocarpic species are not considered here.

I have examined herbarium specimens of the Endogonaceae available in Australia and compared those with fresh fructifications from South Australia and Victoria. I am indebted to Dr J. H. Warcup for collecting much of the fresh material examined in this study and providing notes on their habitats.

Sites and Methods of Collection

Fructifications are formed soon after the onset of autumn rains (May–June) and may be found as late as December provided spring–early summer rains occur. They were found by carefully scraping away litter and surface soil with a small hand-rake. Fructifications were usually covered by a deep layer of moist litter but sometimes a quite thin layer afforded sufficient protection, especially on clay and lateritic soils.

Sites examined were in relatively undisturbed open and low-open eucalypt forest formations (Specht 1972) in South Australia, and in the Grampian Mountains in north-western Victoria, or in exotic pine forests in South Australia.

Many fructifications are small, solitary, inconspicuous, and difficult to differentiate from the litter and soil fragments of their habitat; they were therefore collected only rarely. Sites which yielded fructifications in one year did not necessarily do so in following years. Most of the species were found in the litter layer, although one (*E. crassa*) was more usually found in the soil itself.

It was often impossible to determine in the field what type of fructification had been collected, since in gross morphology most fructifications in the Endogonaceae closely resemble those of other hypogeous fungi. Because of this it has been difficult to determine in most cases whether they are associated with any particular host species in the field (apart from *E. flammicorona*, which was consistently found associated with exotic pines).

Examination of Specimens

Specimens were preserved in formol-acetic-alcohol (FAA: 70% ethyl alcohol, 90 ml: formalin, 5 ml: glacial acetic acid, 5 ml) and/or dried, either in the laboratory for several days or for 24 hr at 60°C. Microscopic preparations consisted of dissections, and sections were cut by hand or with sledge or freezing microtomes. Microtome sections were stained in safranin and light green after dehydration in graded alcohols and xylol (Johansen 1940). Ammoniacal Congo red was routinely used to stain tissues for examination; this was found a particularly good stain for the observation of wall structure. Cotton blue in lactic acid and Melzer's reagent were also useful for differentiating individual structures. In some species the exospore greatly enlarged in Congo red and Melzer's reagent, in which case spore and hyphal dimensions were measured in sections mounted in water. It was sometimes necessary to remove the oil contents of spores and hyphae by immersing sections in acetone for several minutes. This treatment caused some shrinkage and loss of contents of hyphae, but other structures were little affected. Sections of old, dried material were soaked in 5% potassium hydroxide for 20 min to swell the structures to more closely approximate their original dimensions. The developmental changes within a species were followed by first examining immature specimens, then peripheral and central tissue of mature specimens. Individual structures were photographed.

Key to Sporocarpic Species of Endogonaceae in Australia

Chlamydospores are subtended by one hypha, and the spore and sporophore contents are directly connected or divided by a distinct septum. Zygospores are subtended by two hyphae and the endospore is continuous

- | | |
|--|-------------------------|
| 1. Sporocarp containing zygospores | 2. <i>Endogone</i> spp. |
| Sporocarp containing chlamydospores | 6. <i>Glomus</i> spp. |
| 2. Zygospores aggregated in distinct groups | 3 |
| Zygospores not aggregated, scattered throughout fructification | 5 |
| 3. Zygospore wall in one thick (9–22 μ m) layer | <i>E. crassa</i> |
| Zygospore wall in two distinct layers, to 25 μ m together | 4 |
| 4. Gametangia usually widely separated, discrete | <i>E. aggregata</i> |
| Gametangia fused | <i>E. tuberculosa</i> |

5. Zygosporium surrounded by a whorled sheath, in surface view resembling a fingerprint *E. flammicorona*
 Zygosporium surrounded by a ramifying sheath, reticulate in surface view *E. reticulata*
6. Chlamydospore with septum at its base *G. pulvinatus*
 Chlamydospore without septum at its base 7
7. Chlamydospores mostly more than 130 μm in diameter *G. macrocarpus* var. *macrocarpus*
 Chlamydospores less than 130 μm in diameter 8
8. Chlamydospore wall in one thick (3–4 μm) layer, sporophore usually occluded ... *G. tubaeformis*
 Chlamydospore wall in two layers, to 8 μm together, sporophore open *G. tener*

DESCRIPTION OF SPECIES

Genus ENDOGONE Link ex Fr.

1. *Endogone flammicorona* Trappe & Gerdemann 1972: 405, pl. 45, figs. 3, 4; Gerdemann and Trappe 1974: 12, fig. 2.

Figs. 2, 7–13

Endogone lactiflua sensu Fischer 1897: 126; Bucholtz 1912: 155, figs. 1–61, 105–110; Hawker 1954: 436, fig. 1, *k*, *l*; Fassi 1965: 12, fig. 4; non *E. lactiflua* Berk. & Br.

Sporocarps 3 by 24–29 mm in diameter, epigeous, beneath a thick layer of pine needle litter, or hypogeous; without characteristic odour; compact, soft when immature to relatively hard when older, hardening in FAA, drying leathery. Immature sporocarp subspherical, white, or off-white; mature sporocarps usually irregularly lobed or convoluted, sometimes remaining entire, buff to orange brown, sometimes with basal attachment to soil; smooth, felted surface. *Matrix* off-white when immature, later creamy yellow to buff or pale red, without incorporated organic matter; cut surfaces of fresh specimens exude large amounts of a milky, acetone-soluble latex. *Matrix hyphae* loosely woven, regular in diameter, 3–9 μm wide, thin-walled. *Peridium* thin, white, of closely woven, narrow (2–3 μm) hyphae, absent in older fructifications. *Zygosporia* 52–63 by 64–87 μm , pale honey, golden brown and dark brown, not aggregated, globose, subglobose, ellipsoid or obovoid, often angular, usually longer than broad, containing dense oil globules 2–4 μm in diameter. Spore wall in two layers, a thin, yellow exospore (to 1 μm wide) and a thick, hyaline endospore (to 7 μm wide). In Melzer's reagent the exospore stains orange to orange brown while other structures remain unstained. In ammoniacal Congo red the inner spore wall and spore contents are the only structures which take up the bright red stain. *Hyphal mantle* on mature zygosporia of 1–3 layers of closely adhering thick-walled hyphae. The mantle extends up to 25 μm from the spore (Fig. 7) and in surface view resembles a fingerprint (Fig. 8). Occasionally spores abort; as the zygosporium ages the walls fold and collapse away from the thick hyphal web. *Development of the zygosporia*. Progametangia develop as paired, parallel, terminal hyphal swellings, one of which is usually appreciably larger than the other. A septum is laid down separating each gametangium from the suspensor. The suspensors are thin-walled, 30–40 μm broad, curved, occasionally with thin, irregular basal outgrowths. The wall between adjacent gametangia breaks down to form a large pore (Fig. 13). The fused gametangial contents pass into the zygosporium, which develops as an apical outgrowth from the larger gametangium or from fused gametangia (Figs. 10–13). One

or both gametangia may persist as a broad (20–25 μm) basal attachment on the mature zygospore. Hyphae forming the mantle are evident at an early stage as narrow, thin-walled, parallel hyphae in whorls around the spore. Their origin is uncertain.

Specimens Examined. Under *Pinus radiata*, Kuitpo, June, Sept., Oct. 1971, *J. H. Warcup* (ADW 16399, 16400, 16401); Mount Bold, Oct. 1971, *J. H. Warcup* (ADW 16402); under *P. pinaster*, Kuitpo, Nov. 1971, *J. H. Warcup* (ADW 16403); in *Eucalyptus* forest, Echunga, July 1970, *J. H. Warcup* (ADW 16429); Adelaide, Aug. 1971, *J. H. Warcup* (ADW 16404); Iron Bank, July 1970, *J. H. Warcup* (ADW 16430); under *P. radiata*, Mount Gambier and Tantanoola, Nov. 1971, *E. Davison* (ADW 16405, 16406); under *P. radiata*, Mount Bold, Aug. Nov. 1973, *P. Tandy* (ADW 16407, 16408); mixed *Pinus* and *Eucalyptus*, Kuitpo, Aug. 1973, *P. Tandy* (ADW 16409); under *P. radiata*, Mount Bold, Nov. 1973, *B. James* (ADW 16410); under *P. radiata*, Kuitpo, June, July, Aug. 1974, *P. Tandy* (ADW 16431, 16432, 16433); under *P. radiata*, Mount Bold, July 1974, *S. Wigg* (ADW 16434).

Discussion

Endogone flammicorona was segregated as a species distinct from *E. lactiflua* Berk. & Br. by Trappe and Gerdemann (1972). The South Australia sporocarps vary a little from the species description. The gametangia are thick-walled, and one or both may persist as the zygospore matures. Trappe and Gerdemann describe development of zygospores from the tip of the larger gametangium but I have also observed growth from the tip of fused gametangia.

The entire matrix is usually fertile. Growth of the sporocarp is indeterminate so that fragments of litter may be enclosed.

2. *Endogone tuberculosa* Lloyd 1918: 799, fig. 1239; Thaxter 1922: 303–305, figs. 11–16; Cleland and Cheel 1918: 310–11; Gerdemann and Trappe 1974: 24.

Sporocarps 3–10 by 5–12 mm in diameter, epigeous, without latex, compact, hard, irregular, surface rough from closely adhering fine organic particles which give the fructifications the appearance of lumps of light brown soil. *Matrix* bright yellow, composed of groups of spores readily fragmenting, little mycelium visible between the spore groups; often small amounts of incorporated organic matter; some acetone-soluble oils released from cut surfaces. *Matrix hyphae* densely woven, to 13 μm , thin-walled or with thick, smooth walls to 3 μm . *Peridium* not observed. *Zygospores* 44–90 by 68–120 μm , hyaline to pale yellow, densely aggregated in rounded or irregular groups, 400–950 μm in diam., containing 15–60 closely adherent spores; spores very variable in form, subspherical, oval, or irregular from pressure, containing dense granules, sometimes with three or four oil globules 2–5 μm in diam.; spore wall in two layers, a pale yellow exospore to 4 μm wide, and a thin, hyaline endospore 1–2 μm wide. Both wall layers stain red in ammoniacal Congo red while the contents remain unstained. In 5% potassium hydroxide the exospore becomes greatly swollen (to 16 μm) and pushes the endospore into irregular folds. In Melzer's reagent the endospore also becomes slightly swollen, to 4 μm . *Hyphal mantle* not observed. Development of the zygospores not observed. *Gametangia* usually persist as short, straight, thin-walled attachments, 3–4 μm wide.

Specimen Examined. The Rocks, N.S.W., July 1917, *J. B. Cleland* (ADW 2780) (cotype).

3. *Endogone aggregata* sp. nov.

Figs. 3–5, 28, 29

Sporocarpia 6–10 mm diametro, hypogaea, sine latice, compacta et firma, subglobularis vel ellipsoidea, cremea vel crocea; superficies levis vel aspera. *Matrix* lucide crocea vel alba. *Hyphae matrixis* ad 15 μm latae. *Peridium* tenue. *Zygosporae* 78–103 \times 118–182 μm , globosae, subglobosae vel ellipsoideae, cremeae vel croceae, globuli 10–60 aggregati, aggregati globulorum 500–1200 μm diam.; tunica sporae bistratosa, exosporium hyalinum, 5–13 μm late, endosporium hyalinum vel luteolum, 4–12 μm . *Gametangia* discretiae, plerumque insertae late separatae.

Sporocarps 6–10 mm in diameter, hypogeous, without latex or characteristic odour, compact and hard when fresh; small fructifications subspherical and entire, larger ones egg-shaped and slightly lobed, cream to yellow; surface smooth, or rough, from a closely appressed fine layer of organic matter forming a crust. *Matrix* bright yellow, or occasionally white, to the naked eye sometimes appearing smooth and continuous, or more usually disjunct, with distinct groups of spores separated by narrow bands of dense white hyphae; both types readily fragmenting on drying. Various degrees of spore aggregation are exhibited even within the same fructification. *Matrix hyphae* densely woven, broad (to 15 μm), thin-walled or with thick (2–5 μm) smooth walls, branching frequently, sometimes with three or four branches arising close together from an enlarged hypha. *Peridium* thin, of thin-walled highly compressed hyphae, absent in patches. *Zygosporae* 78–103 by 118–182 μm , cream to yellow, aggregated, in rounded or irregular spore groups, containing 10–60 spores which are not readily separable from each other, spores spherical, subspherical, or elliptical, occasionally angular from pressure, initially containing fine granules, the contents later becoming crystalline or with dense oil globules 2–7 μm in diameter. Spore groups 500–1200 μm in diameter. Spore wall in two distinct thick layers, a hyaline exospore 5–13 μm wide, continuous with the gametangial wall, and a hyaline to pale yellow endospore 4–12 μm wide, sometimes forming short protrusions into the exospore (Fig. 5). In ammoniacal Congo red and cotton blue the endospore and spore contents stain more intensely than the exospore. In 5% potassium hydroxide and in ammoniacal Congo red the exospore becomes greatly swollen (to 19 μm thick) and pushes the endospore into irregular folds (Fig. 28). *Hyphal mantle* not observed. *Development of zygosporae* not observed. *Gametangia and suspensors* persistent, the gametangia sometimes inserted close together, more usually widely separated to almost opposite each other; suspensors bulbous or straight, with thick, smooth walls.

Specimens Examined. *Eucalyptus* forest, Kuitpo, June 1970, J. H. Warcup (ADW 16411); Echunga, July 1970, J. H. Warcup (ADW 16412); Grampian Mountains, Vic., July 1971 (on burnt site), J. H. Warcup (ADW 16413); Mount Crawford, June 1973, J. H. Warcup (ADW 16414).

Etymology. Latin, 'aggregatus' (clustered), referring to the grouping of the spores.

Discussion

This species resembles *E. stratosa* Trappe, Gerdemann & Fogel (Gerdemann and Trappe 1974) in spore size (78–182 μm in *E. aggregata*, 82–122 μm in *E. stratosa*) and in bearing two discrete gametangia. However, sporocarps of *E. aggregata* are

compact, with spores usually clearly aggregated, while sporocarps of *E. stratosa* are stratified and irregular, with spores arranged either randomly or in irregular groups. The matrix hyphae are also different; in *E. stratosa* they are thin-walled and vesicular, while in *E. aggregata* they are more usually thick-walled and brittle.

In these sporocarp and matrix hyphae characters *E. aggregata* is similar to *E. multiplex* Thaxter: however, the spores in *E. aggregata* are larger (78–182 μm) than *E. multiplex* (48–125 μm) and the spore groups (500–1200 μm) are also larger (350–700 μm in *E. multiplex*).

The colour of the sporocarp is not a very reliable taxonomic character. Most of the specimens were a distinctive bright yellow but some fully mature specimens were found which were white.

The exospore in members of the Endogonaceae is usually relatively thin but in *E. aggregata* it was unusually wide (to 13 μm). Thaxter (1922) also reports a thick endospore in *E. multiplex* (8–10 μm).

4. *Endogone reticulata* sp. nov.

Figs. 14–18

Sporocarpia 7 \times 5 mm, epigaea, sine latice, compacta et tenera, subglobosa, leviter lobata, rubra quando dulcis, pallescens in subroseam luteam, cuius superficies aspera. *Matrix* diluta rosea; pagina incisa exudans aliquot guttas olei. *Hyphae matricis* 4–8 μm , plerumque angusta parietibus tenuibus, tumoribus irregularibus, intercalariibus et terminalibus vesicularibus. *Peridium* tenuum, hypharum complanatarum. *Zygosporae* 69–90 \times 92–103 μm , luteae, nec aggregatae, globosae vel ellipsoideae. Tunica sporae bistratosa, exosporium tenuum, atroluteum, 1–2 μm late, et endosporium crassum, hyalinum, 4–8 μm late. Palla hypharum 1–2 stratosum, hypharum late (5–12 μm), quae arte adpressae parietibus tenuibus. *Gametangia* parallela vel apposita, lata, 20–46 μm , subaequalia. Orificium gametangii sporae est multum proprium, 18–24 μm latitudine.

Holotype. Iron Bank, S.A., J. H. Warcup (ADW 16415).

Sporocarp. 7 by 5 mm, epigeous, in eucalypt litter, without latex, compact, soft when fresh, hardening in FAA, subspherical, slightly lobed, with basal attachment to soil, brick red when fresh, fading to pinkish yellow in FAA, surface rough. *Matrix* pale red, without incorporated organic matter, cut surfaces exuding a small amount of acetone-soluble oils. *Matrix hyphae* 4–8 μm wide, loosely woven, thin-walled, with irregular intercalary and terminal thin-walled vesicular swellings. Interspersed with these are broad (to 15 μm), branching lengths of hyphae with smooth, thick (2–4 μm), regular walls (Fig. 18). *Peridium* thin, of flattened hyphae, absent in some areas. *Zygosporae* 69–90 by 92–103 μm , yellow, not aggregated, globose, ellipsoidal, or angular from pressure, containing fine granules or dense oil globules 1–3 μm in diam. Spore wall in two layers, a thin, dark yellow exospore 1–2 μm wide, and a thick, hyaline endospore 4–8 μm wide. In ammoniacal Congo red the endospore becomes slightly swollen and appears laminated, up to seven layers, the innermost of which stains very readily while the remainder stain more slowly. In Melzer's reagent the exospore stains orange. *Hyphal mantle* of 1–2 layers of closely appressed, wide (5–12 μm), thin-walled hyphae, not readily separable from the spore, arising as apical

outgrowths from the gametangium. Initially the hyphae lie parallel around the base of the spore, later ramifying over the lateral and upper surfaces (Fig. 16). *Gametangia* parallel or apposite, wide (20–46 μm), subequal, without basal hyphal outgrowths. *Suspensors* thin-walled, and curved. *Development of the zygospores*. The walls between adjacent gametangia break down and contents fuse, the zygospore developing from the apex of the fused portion, or laterally (Figs. 14, 15). The endospore and gametangial walls thicken and the walls of the mantle hyphae also become thickened on all faces, forming a mantle with a square to rectangular pattern in longitudinal section. Remnants of either or both gametangia usually persist as thick-walled attachments. The junction of the gametangium and spore is unusually wide, 18–24 μm (Fig. 16).

Specimen Examined. Holotype, in eucalypt litter, Iron Bank, July 1970, J. H. Warcup (ADW 16415).

Etymology. Latin, 'reticulatus' (netted), referring to the appearance of the hyphal sheath.

Discussion

This species has several distinctive features which have not been previously reported for other species of *Endogone*. The most striking is its brick-red colour; no other *Endogone* fructification has been recorded which is any shade other than white, yellow, or brown. One *E. lactiflua* fructification (synonym *E. rosea*, Zeller 1941, fide Trappe and Gerdemann 1972) was described as having a rosy pink interior but the exterior was grey.

Several species of *Endogone* have zygospores enclosed in a more or less closely appressed hyphal sheath (*E. flammicorona*, *E. lactiflua*, *E. multiplex* and *E. stratosa*). The form of the sheath in *E. reticulata* is unusual in that the hyphae are wide (5–12 μm), thin-walled and loosely woven. The very wide junction (18–24 μm) of the gametangium at the base of the spore has not been reported for any other species.

Similar vesicular matrix hyphae have been described by Gerdemann and Trappe (1974) in *E. lactiflua*, *E. stratosa*, *E. pisiformis* Link ex Fries, *E. incrassata* Thaxter, and *E. oregonensis* Gerdemann & Trappe.

5. *Endogone crassa* sp. nov.

Fig. 6

Sporocarpium 4 × 2 mm, epigaea, sine latice, compacta et firma, eburnea, superficies aspera et irregularis ob sporas aggregatus projectas. *Matrix* luteola. *Hyphae matrixis* plerumque tenues (ad 5 μm), interspersa interdum latis hyphis. *Peridium* tenue. *Zygosporae* 83–92 × 102–152 μm , luteolae, dispositae turmas sporarum, 350–550 μm diametro, continentes 3–12 spora. Spora sphaericae vel angulares. Spora tunica crassa, 9–22 μm , continua parietis gametangio. *Gametangia* discreta, aequalis, inserta approximata vel late separata, cum parietibus crassis propriis, 4–10 μm latitudine.

Holotype. Loftia Park, S.A., J. H. Warcup (ADW 16416).

Sporocarp 4 by 2 mm, epigeous, in litter, without latex; compact and firm when fresh, drying waxy and with edges curling over towards the central axis, off-white,

surface irregular from projecting spore groups. *Matrix* pale yellow, without incorporated organic matter. *Matrix hyphae* mostly narrow (to 5 μm) and highly compressed, interspersed with occasional thin-walled, wide (9–12 μm) hyphae. *Peridium* thin, of highly compressed hyphae. *Zygosporae* 83–92 by 102–152 μm , pale yellow, aggregated in more or less spherical or irregular spore groups, 350–550 μm in diameter, containing 3–12 spores in each group; the groups enclosed by bands of thin-walled, compressed hyphae. Spore subspherical or angular, often triangular in section, crystalline, sometimes with black inclusions. Spore wall thick (9–22 μm), the inner surface often slightly indented, the wall continuous with the thickened walls of the gametangia. In ammoniacal Congo red and 5% potassium hydroxide solution the wall becomes slightly swollen and appears to be laminated, to seven layers. In cotton blue–lactic acid the spore contents and mature hyphae stain dark blue, while the wall stains pale blue. *Hyphal mantle* not observed. *Gametangia and suspensors* persistent, discrete, equal, at wide angles, usually inserted close together but sometimes widely separated, each with distinctive, thick walls, 4–10 μm wide.

Specimen Examined. Holotype, in *Eucalyptus* forest, Loftia Park, S.A., Sept. 1969, *J. H. Warcup* (ADW 16416).

Etymology. Latin ‘crassus’ (thick), referring to the thick-walled zygosporae and gametangia.

Discussion

This species was found only once, in 1969. It has several unusual features. Such thick-walled gametangia have only been reported once elsewhere, by Godfrey (1957) in zygosporae of *Glomus microcarpus*. Godfrey considered this wall thickening abnormal, but in *E. crassa* the thickening of the gametangial and zygosporae walls was observed in all zygosporae.

The spore groups in *E. crassa* are more distinct than in any of the other species with spore aggregations I have examined. The zygosporae appears to develop from the fused upper portions of the gametangia, but this could not be determined with certainty.

Genus GLOMUS Tul. & Tul.

1. *Glomus macrocarpus* Tul. & Tul. var. *macrocarpus*.

Figs. 1, 19–22

Endogone macrocarpa Tul. & Tul. Tulasne and Tulasne 1851: 182, fig. 1; Schröter 1889: 260; Saccardo 1889: 906, nr. 3593; Fischer 1897: 125; Cooke 1892: 248, nr. 1350; Bucholtz 1902: 81; Bucholtz 1907: 447; Bucholtz 1912: 184, figs. 62–74; Thaxter 1922: 312; Knapp 1952: 86; Hawker 1954: 441, fig. 2, *a–g*; Godfrey 1957: 119; Lange and Lund 1954: 91, fig. 1.

Endogone australis Berkeley 1860: 282, pl. 183, fig. 15, fide Thaxter 1922.

Paurocotylis fulva var. *zealandica* Cooke 1879: 59, fide Gerdemann and Trappe 1974.

Endogone versiforme Karsten 1884: 39, fide Gerdemann and Trappe 1974.

Endogone pampalonia Baccarini 1903: 79, fide Thaxter 1922.

Endogone tenebrosa Thaxter 1922: 314, fide Nicolson and Gerdemann 1968.

Endogone guttulata Fischer 1923: 85, fide Gerdemann and Trappe 1974.

Endogone nuda Petch 1925: 322, fide Gerdemann and Trappe 1974.

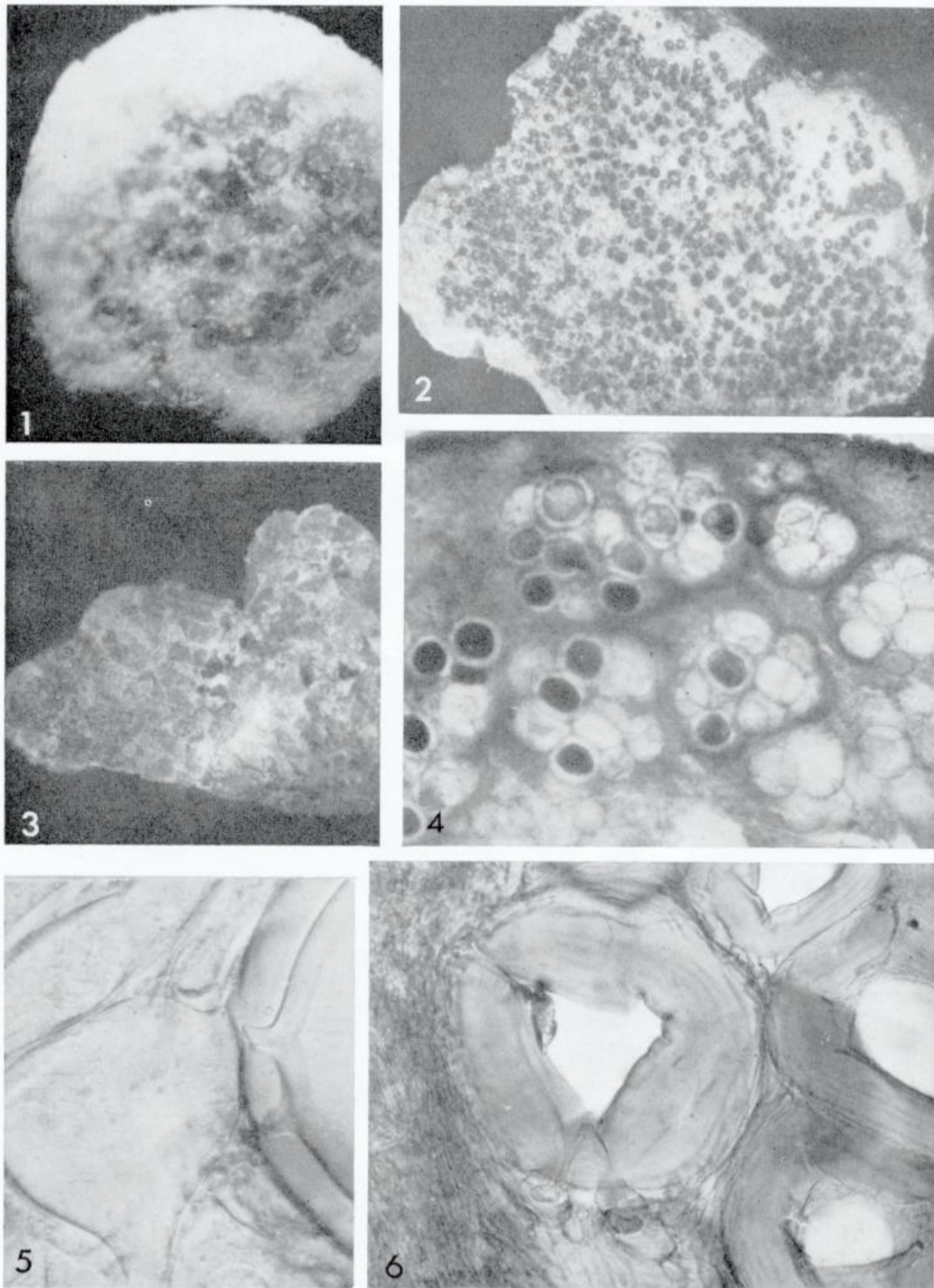
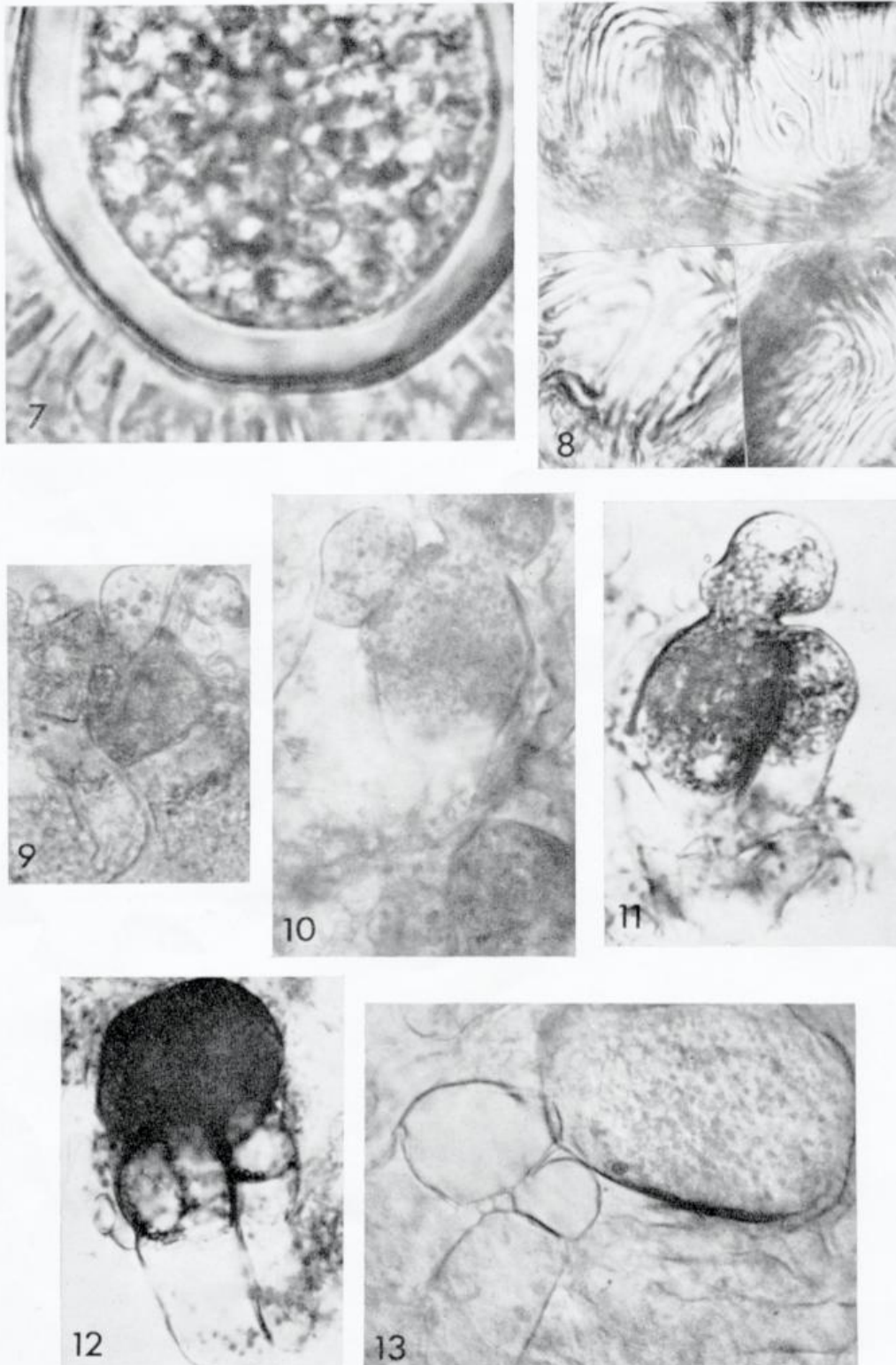
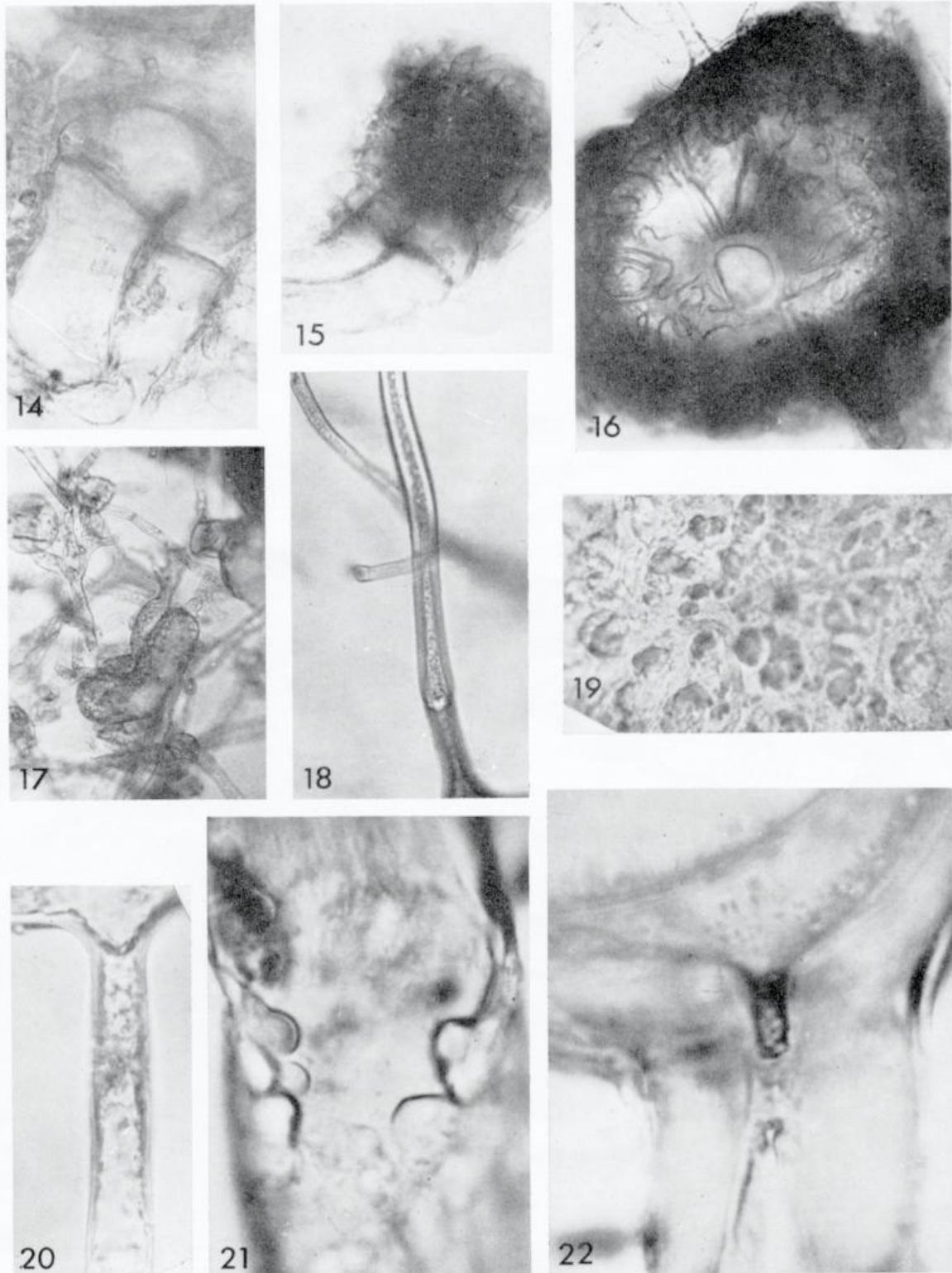


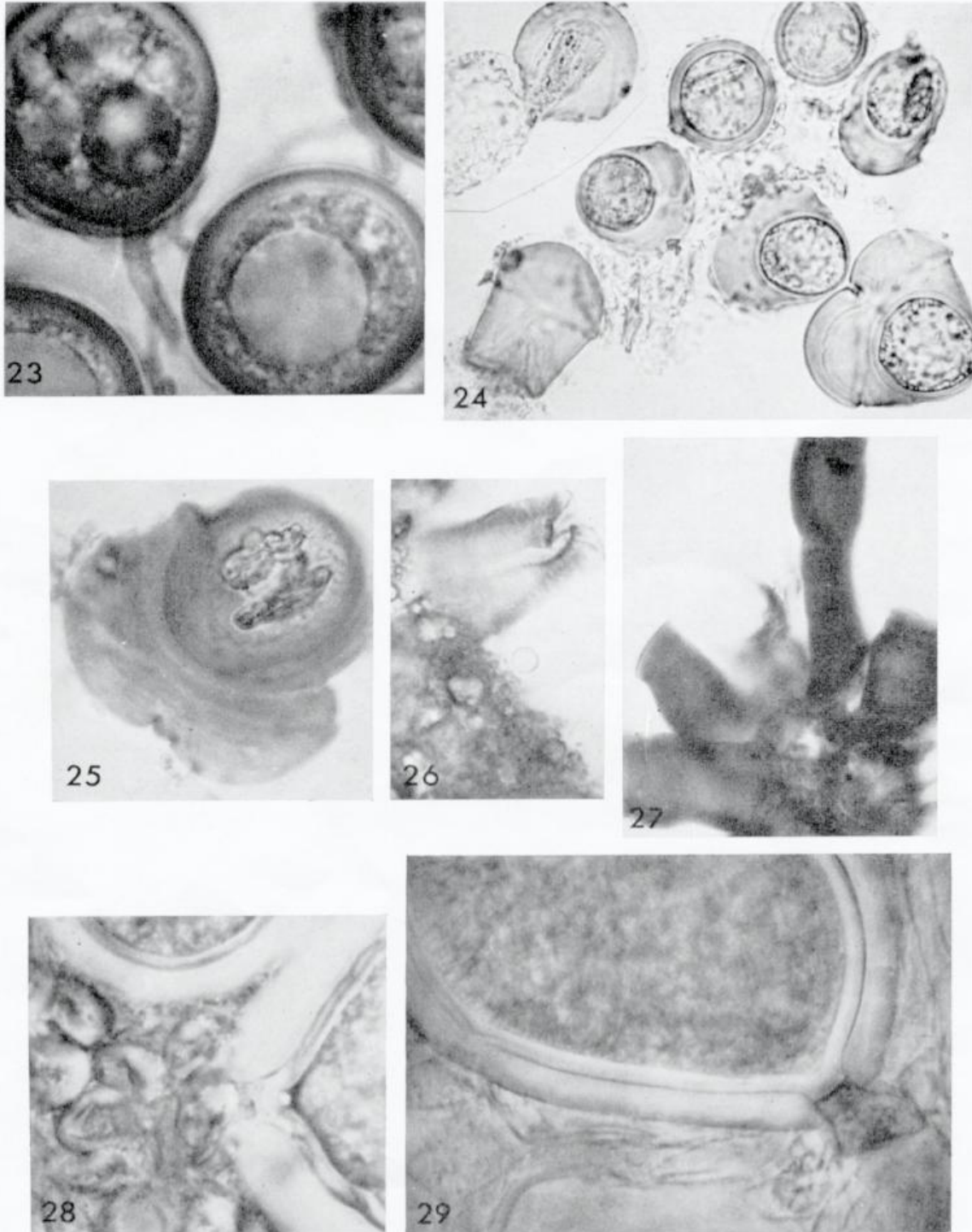
Fig. 1. *Glomus macrocarpus* var. *macrocarpus*. Cut surface of fructification with loosely embedded chlamydospores, wide peridium. Fig. 2. *Endogone flammicorona*. Cut surface of fructification, with granular zygospores, thin peridium. Figs. 3–5. *E. aggregata* sp. nov. Fig. 3. Cut surface of fructification, showing zygospores aggregated in distinct spore groups. Fig. 4. Detail of spore groups, each surrounded by a narrow band of hyphae. Fig. 5. Zygospore with bulbous suspensor. The endospore forms short protrusions into the exospore. Fig. 6. *E. crassa* sp. nov. Zygospore with thick-walled gametangia.



Figs. 7–13. *Endogone flammicorona*. Fig. 7. Zygospore and sheath in section. Fig. 8. Surface view of sheath, showing distinctive fingerprint pattern of thickened hyphae. Figs. 9–13. Development of the zygospore. Fig. 9. Gametangia and suspensors. Fig. 10. Fusion pore between gametangia. Fig. 11. Growth of zygospore from larger gametangium. Fig. 12. Growth of zygospore from fused gametangia. Fig. 13. Immature zygospore with wall separating it from gametangia.



Figs. 14–18. *Endogone reticulata* sp. nov. Fig. 14. Fusion of gametangia. Fig. 15. Immature zygospore with beginnings of the hyphal sheath. Fig. 16. Mature zygospore, showing wide junction at base of the spore, and wide, thin-walled hyphae of netted sheath. Fig. 17. Vesicular matrix hyphae. Fig. 18. Board matrix hyphae with thick, smooth walls. Figs. 19–22. *Glomus macrocarpus* var. *macrocarpus*. Fig. 19. Surface of mature chlamyospore showing ornamentation. Fig. 20. Matrix hyphae with irregularly thickened walls. Fig. 21. Globose thickenings of wall of sporophore. Fig. 22. Detail of junction of spore and sporophore showing bridge formed by thickened walls of sporophore.



Figs. 23–27. *Glomus tubaeformis* sp. nov. Fig. 23. Mature chlamydospores. Figs. 24–27. Development of trumpet-shaped cells. Fig. 24. Cells in various stages of development, some extruding contents. Fig. 25. Basal constriction of chlamydospore into two chambers. Fig. 26. Constricted apex of cell. Fig. 27. Fully developed, elongated cells without contents. Figs. 28, 29. *Endogone aggregata* sp. nov. Fig. 28. Thick-walled matrix hyphae in section, and swollen exospore pushing endospore into irregular folds (in ammoniacal Congo red). Fig. 29. Mature zygospore with discrete gametangia.

Sporocarps 2–10 mm broad, epigeous, in litter, without latex or characteristic odour, compact or amorphous, firm or soft when fresh, not hardening in FAA, sub-spherical and creamy white, with distinct basal attachment to soil; or irregular, off-white; older specimens may be yellow to pale brown; surface smooth, or rough from loose encrustation of organic matter. *Matrix* creamy to pale yellow, consisting of a few large (133–291 μm in diameter) firmly embedded spores; sometimes with abortive spores scattered throughout fructification, incorporated organic matter absent to extensive. *Matrix hyphae* loosely woven, 6–15 μm wide, branching at wide angles, fragile and breaking readily into fragments consisting of three or four branches; thin-walled, or with irregular thickening, to 3 μm ; sometimes the hyphal thickening takes the form of characteristic, internal globose protrusions especially in the sporophore (Fig. 21); septa few, sometimes delimiting hyphae with contents from empty hyphae. *Peridium* absent, thin, or wide, of hyphae similar to matrix hyphae. *Chlamydospores* 122–291 μm in diameter, at first hyaline, becoming cream, yellow, brown to dark brown, not aggregated, globose, subglobose, or slightly dented from pressure (especially young, thin-walled spores). Contents yellow, at first finely and evenly granular, later with many small or two or three large oil globules. Spore wall up to 10 μm thick, in two layers; a thin, hyaline to yellow, rough exospore 2 μm thick, and a smooth orange-brown endospore, which is at first thin but becomes considerably thickened especially at the junction of spore and sporophore where it forms a laminated plug. The endospore is continuous with the inner layer of sporophore for a short distance below the junction of the spore. The junction of the spore and sporophore is at first open; as the endospore thickens towards the centre this junction decreases until finally only a few narrow channels are present in the plug, or it may become entirely occluded (Fig. 22). Fine radial canals are present in the walls of some spores, often associated with large oil globules in the spore. The external surfaces both of spores and matrix hyphae are frequently ornamented, sometimes presenting a striated appearance. The hyphae are also mucilaginous and may become encrusted with organic materials. In ammoniacal Congo red the surface ornamentation and exospore stain bright red, while the endospore and the globose internal thickenings remain unstained. In zinc chloro-iodide the exospore stains orange-brown and the endospore pale orange. *Hyphal mantle* not observed.

Development. The chlamydospores develop as globose or pyriform swellings, terminal on short or long, straight or slightly curved sporophores, which are slightly tapering towards the base, or regular. The young spores are thin-walled and fragile and readily crack under light pressure in characteristic fracture lines. Both developing and mature spores are usually found in close proximity.

The protoplasm of both spores and hyphae is under considerable pressure, oozing thickly and rapidly from cut ends of sporophores and matrix hyphae and through the fine radial canals in the endospore. The flow is particularly evident in fresh material, but is still rapid even in material which has been dried for some time.

Specimens Examined. *Eucalyptus* forest, Iron Bank, Sept. 1969, *J. H. Warcup* (ADW 16417); Loftia Park, Sept. 1969, *J. H. Warcup* (ADW 16418); Belair National Park, July, Oct. 1971, *J. H. Warcup* (ADW 16420, 16421); Adelaide, Aug. 1972, *J. H. Warcup* (ADW 16422); Mount Crawford, Oct. 1971, June 1973, *J. H. Warcup* (ADW 16423, 16424). TASMANIA (*L. Rodway* 352A/351): Fern Tree, May 1912; Mount Nelson, Sept. 1919; Cascades, July 1910, May 1923, July 1928; Newtown Creek, Apr. 1923. Tasmanian specimens identified by J. M. Trappe in 1971.

Discussion

The South Australian and Tasmanian specimens of *Glomus macrocarpus* var. *macrocarpus* show great variability in sporocarp size and form, coherence and colour, spore size, colour and wall thickness, and amount of adhering and included organic matter. The material, however, does not fall into clearly distinct types; rather it would appear that *G. macrocarpus* var. *macrocarpus* is a variable taxon, with representatives grouped discontinuously.

Variations in fructification form, colour and amount of adhering dirt are probably a function of habitat. Spore colour may be an expression of maturity, but this is not always a very reliable parameter. Although dark spores are generally older (as suggested by wall and plug thickness) than light-coloured spores, yellow spores in particular may be either mature or immature.

The Australian material most closely resembles that described by Bucholtz (1912) and Thaxter (1922) (as *Endogone macrocarpa*). The chlamydospores are larger (to 291 μm) than those described by Gerdemann and Trappe (1974) (93–230 μm), and more variable in colour.

Abortive spores have also been reported in Danish specimens (Lange and Lund 1954). The distinctive globose thickening on the sporophore (Fig. 21), and sticky outer surface of spores and hyphae have not been described elsewhere. This sticky layer did not stain with alcian blue (Reiss 1971) and is probably not extracellular mucilage.

Thaxter (1922) suggested that *G. macrocarpus* was the chlamydosporic stage of *E. lactiflua* (= *E. flammicorona*). I have observed *G. macrocarpus* type hyphae in South Australian *E. flammicorona*; however, *G. macrocarpus* and *E. flammicorona* are not found in the same sites (Warcup, personal communication).

2. *Glomus pulvinatus* (P. Henn.) Trappe & Gerdemann 1974: 59; Lloyd 1918: 800, fig. 1240); Thaxter 1922: 319, figs. 41–43; Gerdemann and Trappe 1974: 36.
Endogone pulvinata P. Hennings 1897: 212.

Sporocarps 5–13 mm, without latex, compact, firm, subspherical, pale yellow, sometimes with basal attachment to soil, readily fragmenting on drying, surface smooth, with a little adherent organic matter and mosses. *Matrix* yellow, under low magnification consisting of pale yellow spores loosely embedded in white hyphal matrix; without incorporated organic matter; small amounts of acetone-soluble oils released from the cut surface. *Matrix hyphae* loosely woven, thin-walled, broad (7–27 μm), sometimes with bulbous expansions but more usually regular, branching at wide angles with hyphae swollen where branches arise, contents finely granular. *Peridium* thin, of hyphae similar to matrix. *Chlamydospores* 53–90 by 55–93 μm in diameter, golden yellow, not aggregated, fairly regularly spherical, sometimes slightly pyriform, the fragile, thin-walled (2–4 μm) spores often dented from pressure; contents yellow, densely granular, often absent. Spore wall in two thin layers, a hyaline to pale yellow slightly roughened exospore 1 μm thick, and a hyaline to pale yellow, smooth endospore to 3 μm . A smooth, pale yellow septum to 1 μm thick separates the spore from the sporophore, which is wide (12–17 μm), long, straight or with a bulbous expansion below the spore, thin-walled (1 μm), sometimes slightly thickened close to the septum, often constricted at the junction with the spore.

In ammoniacal Congo red both exospore and endospore stain red and contents remain unstained. In Melzer's reagent the contents stain yellow-brown while the walls remain unstained. No hyphal mantle was observed on the spores.

The chlamydospore develops as a terminal globose or pyriform swelling on the sporophore, both mature and developing spores being found in close proximity in the fructifications.

Specimens Examined. McRobies Gully, near Cascades, Tas., Mar. (?) 1917, *L. Rodway*.

Discussion

The Tasmanian specimens of *G. pulvinatus* are similar to those described by Lloyd (1918) and Thaxter (1922), although Gerdemann and Trappe (1974) describe single-walled spores. The Tasmanian material more closely resembles *G. fragilis* (Berk. & Br.) Trappe & Gerdemann in wall structure and wall size; however, the spores (53–93 μm) and sporophores (12–17 μm) in *G. pulvinatus* are larger than in *G. fragilis* (spores 53–73 μm , sporophores to 13 μm).

The septum at the base of the spore is almost invariably present in the Tasmanian material, even in young spores, and is a distinctive taxonomic feature. The matrix hyphae are wider (to 27 μm) than in any of the other Endogonaceae I have examined, and the walls do not have the thickening characteristic of such wide hyphae in such species as *G. macrocarpus*.

3. *Glomus tubaeformis* sp. nov.

Figs. 23–27

Sporocarpia 3–8 mm, epigaea, sine latice, compacta et firma, irregularis, alba. *Matrix* alba. *Hyphae matrixis* 1–2 μm late, sinuolatae. *Peridium* tenue. *Chlamydosporae* 23–28 \times 31–35 μm , albae, nec aggregatae, subglobosae vel ellipsoideae, spora tunica crassa, 3–4 μm , saepe continuum. *Matrix* saepe interspersa cellulis costatis cavis buccinatis.

Holotype. *Eucalyptus* forest, Mount Crawford, June 1973, *J. H. Warcup* (ADW 16426).

Sporocarps 3–8 mm at widest point, epigeous, without latex or characteristic odour, compact, firm when fresh, irregular, white, sometimes darkening on drying, sometimes with a distinct basal attachment to the soil, composed of thin (1–2 μm), double-walled, highly refractive hyphae; surface hard, regular, composed of a layer of narrow (1 μm), sinuous, highly refractive hyphae projecting at right angles. *Matrix* white, consisting of densely packed crystalline spores, with little evidence of matrix hyphae; usually without incorporated organic matter but in one fructification with bands of fine organic material. *Matrix hyphae* very compressed, somewhat sinuous, branching frequently, with slight swellings where branches arise, slightly irregular, 1–2 μm , highly refractive, containing small oil globules. *Peridium* thin, of closely woven, thin (1–2 μm) hyphae. *Chlamydospores* 23–28 by 31–35 μm , white, not aggregated, subspherical to elliptical, sometimes distorted and irregular; contents at first granular, later with many small oil globules which may coalesce to form one large drop occupying most of the cell (Fig. 23). Spore wall forming one thick (3–4 μm), highly

refractive layer. Sometimes the wall extends almost to the centre of the spore (to 15 μm thick), and cytoplasmic contents have disappeared. In most spores the wall is continuous but in some a narrow channel connects the protoplasm of the spore and sporophore. The spores are terminal on long, straight, suspensor hyphae, which are at first thin-walled, later becoming very thick-walled and similar in appearance to the spore wall. Both sporophore and spore walls stain bright red in ammoniacal Congo red. No hyphal mantle was observed on the spores.

In all the Australian specimens examined a most unusual feature was observed: ribbed, hollow, trumpet-shaped cells staining very deep red in ammoniacal Congo red. They were usually found interspersed with chlamydospores although in some areas they occurred in groups. It is difficult to determine how such structures develop or what they represent. It appears that successive layers of wall material are laid down on one face of chlamydospores so that they become expanded lengthwise. The cytoplasm is forced towards the other end of the cell and extruded through the opening (perhaps the original point of attachment of a suspensor hypha) (Fig. 24). The bulbous base of the spore may become constricted into two portions, with a central wall dividing the hollow interior into two chambers along the long axis of the cell (Fig. 25). In what is apparently the final stage of their formation the cells often form a curved lip surrounding the opening of the apex (Fig. 26).

Specimens Examined. *Eucalyptus* forest, Iron Bank. Sept. 1969, *J. H. Warcup* (ADW 16425); Mount Crawford, June 1973, *J. H. Warcup* (ADW 16426) (holotype); under grasses, Mount Crawford, June 1973, *J. H. Warcup* (ADW 16427).

Etymology. Latin, 'tubaeformis' (trumpet-shaped).

Discussion

It is difficult to distinguish zygosporangia from chlamydospores when the spore wall is continuous. A continuous endospore usually indicates that the spore is a zygosporangium, although it may also result from thickening of the walls of the sporophore in chlamydosporic forms. In most of the spores in *G. tubaeformis* the opening was entirely occluded. Godfrey (1957) and Gerdemann and Trappe (1974) similarly describe nearly or entirely occluded chlamydospores in *G. microcarpus*.

The peculiar trumpet-shaped cells (Figs. 26, 27) have not been reported elsewhere in the Endogonaceae, nor in any other fungus as far as I am aware. Their function is unknown. Sometimes all the chlamydospores in one area have been converted to these peculiar structures.

4. *Glomus tener* sp. nov.

Sporocarpia 2–10 mm, epigaea, sine latice, amorphica, mollissima, irregularis et leviter complanata, crocea brunnea, pagina mollis. *Matrix* crocea brunnea. *Hyphae matrixis* 5–18 μm late, interdum constrictae. *Peridium* nec continuum, hypharum laticum, lutearum, complanatarum. *Chlamydosporae* 44–130 μm , brunneae, nec aggregatae, globosae vel leviter pyriformiae, quarum contenta densissima granulata. Spora tunica bistratosa, exosporium (1 μm) asperum hyalinum tenue, et endosporium leve hyalinum (ad 7 μm). Nec ullum septum fundo sporae. Sporophorae longae et regularae, vel breves et ramosae, 8–12 μm latitudine, quae plerumque constricta parum conjuncta spora.

Holotype. Mount Crawford, S.A., *J. H. Warcup* (ADW 16428).

Sporocarps 2–10 mm wide, epigeous, without latex or characteristic odour, amorphous, very soft when fresh and not hardening in FAA, fragmenting on drying, irregular and slightly flattened, orange-brown when fresh, becoming dark brown in FAA; surface soft. *Matrix* orange-brown, with little incorporated organic matter. Under low magnification consisting of shiny, translucent spores loosely embedded in the hyphal matrix, darkening to yellow-brown on drying. *Matrix hyphae* loosely or closely woven (5–18 μm), mostly thin-walled although sometimes walls slightly thickened, with densely granular contents and a few oil globules which exude slowly from cut ends, sometimes constricted, rarely septate. *Peridium* not continuous, some areas covered by a loosely woven web of wide, yellow flattened hyphae. *Chlamydospores* 44–130 μm in diameter, yellow, pale orange or brown, not aggregated, fairly regularly globose or somewhat pyriform, with very dense granular contents, sometimes with a few oil globules. Spore wall in two thin layers, a rough, hyaline, thin (1 μm) exospore frequently with adhering debris, and smooth, hyaline endospore, slightly and irregularly thickened (to 7 μm). The wall cracks under light pressure. There is no septum at the base of the spore. In ammoniacal Congo red the exospore stains bright red while the endospore and suspensor hypha remain unstained.

No hyphal mantle was observed on the spores. The spores develop as terminal globose swellings on long and regular, or short and branched sporophores, 8–12 μm wide, usually slightly constricted at the junction with the spore. Both developing and fully formed spores are found together.

Specimen Examined. Holotype under grasses, Mount Crawford, June 1973, J. H. Warcup (ADW 16428); *Eucalyptus* forest, Iron Bank, Sept. 1974, J. H. Warcup (ADW 16435).

Etymology. Latin, 'tener' (soft-textured).

Discussion

This species has unusually soft and amorphous sporocarps, and chlamydospores and matrix hyphae with very dense contents. Protoplasm streams less freely from cut hyphae than in other Endogonaceae, perhaps because of the dense contents. *Glomus tener* resembles *G. fragilis* (Berk. & Br.) Trappe & Gerdemann in sporophore dimensions and wall structure; however, no septa at the base of the spores in *G. tener* were observed, even after the contents had been cleared by several days' immersion in 15% potassium hydroxide.

Acknowledgments

I wish to thank Drs P. H. B. Talbot and J. H. Warcup for criticism of the manuscript; the Botany Department in the University of Tasmania for specimens from Tasmania; Miss J. Manders for the Latin descriptions and Dr Helga Clark for help with German translations. The author was supported during the study by a Commonwealth Post-graduate Award.

References

- Baccarini, P. (1903). Spora i caratteri di qualche *Endogone*. *Nuovo G. Bot. Ital.* **10**, 79–92.
- Berkeley, M. J. (1860). Flora Tasmaniae. In 'The Botany of the Antarctic Voyage of H. M. Discovery Ships 'Erebus' and 'Terror' in the years 1839–43 under the command of Captain Sir James Clark Ross, R.N., F.R.S.', ed. J. D. Hooker, part III, vol. 2, 422. (Lovell Reeve: London.)
- Bevege, D. I. (1971). Vesicular-arbuscular mycorrhizas of *Araucaria*; aspects of their ecology and physiology and role in nitrogen fixation. Ph.D. Thesis, Univ. of New England.

- Bevege, D. I., and Richards, B. N. (1971). Some aspects of *Endogone* forming mycorrhizas with hoop pine (*Araucaria cunninghamii* Ait.). 15th Congr. Int. Union For. Res. Organs., Sect. 24, Gainesville, Fla., 1971.
- Bucholtz, F. (1902). Beiträge zur morphologie und systematik der hypogaeen (Tuberaceen und Gastromyceten pr. p.) nebst Beschreibung aller bis jetzt in Russland angetroffenen Arten. (Aus. d. Naturhist. Museum d. Grafen K. P.) In 'Scheremetjeff in Michailowskoje Gouvernem. Moskau, vol. 1, 80-3.
- Bucholtz, F. (1907). Zweiter Nachtrag zur Verbreitung der Hypogaeen in Russland. *Bull. Soc. Nat. Moscou* 447-8.
- Bucholtz, F. (1912). Beiträge zur Kenntnis der Gattung *Endogone* Link. *Beih. bot. Zbl.* **29**(2), 147-224.
- Cleland, J. B., and Cheel, E. (1918). Australian fungi: notes and descriptions (3). *Trans. R. Soc. S. Aust.* **43**, 262-315.
- Cooke, M. C. (1879). New Zealand fungi. *Grevillea* **8**, 54-68.
- Cooke, M. C. (1892). 'Handbook of Australian Fungi.' (Williams & Norgate: London.)
- Fassi, B. (1965). Micorrize ectotrofiche di *Pinus strobus* L. prodotte un'endogone (*Endogone lactiflua* Berk.). *Allionia (Turin)* **11**, 7-15.
- Fischer, E. (1897). Ascomyceten: Tuberaceen und Hemiasceen. Rabenhorst's Kryptogamen. In 'Flora von Deutschland, Oesterreich und der Schweiz', Aufl. 2, **1**(5), 1-131.
- Fischer, E. (1923). *Endogone*, eine Gattung der unterirdischen Pilze. *Schweiz. Z. Pilzkd.* **1**, 85-7.
- Gerdemann, J. W., and Trappe, J. M. (1974). The Endogonaceae in the Pacific Northwest. Mycol. Mem. No. 5. (New York Bot. Gard.)
- Godfrey, R. M. (1957). Studies of British species of *Endogone*. 1. Morphology and taxonomy. *Trans. Br. Mycol. Soc.* **40**(1), 117-35.
- Hawker, L. E. (1954). British hypogeous fungi. *Philos. Trans. R. Soc. Lond. Ser. B. Biol. Sci.* **237**, 429-546.
- Hennings, P. (1897). Beiträge zur Pilzflora Sudamericas, II. *Hedwigia*, p. 211.
- Johansen, D. A. (1940). 'Plant Microtechnique.' (McGraw-Hill Book Co.: New York.)
- Karsten, P. A. (1884). *Fragm. Mycol.* **23**, 39-40.
- Knapp, A. (1952). Die eurapaischen Hypogaeen-Gattungen und ihre Gattungstypen. *Schweiz. Z. Pilzkd.* **30**(6), 81-92.
- Lange, M., and Lund, E. M. (1954). The genus *Endogone* in Denmark. *Friesia* **5**(1), 90-5.
- Lloyd, C. J. (1918). *Mycol. Notes* **56**, 799-800.
- Mosse, B., and Bowen, G. D. (1968a). A key to the recognition of some *Endogone* spore types. *Trans. Br. Mycol. Soc.* **51**(3 and 4), 469-83.
- Mosse, B., and Bowen, G. D. (1968b). The distribution of *Endogone* spores in some Australian and New Zealand soils, and in an experimental field soil at Rothamsted. *Trans. Br. Mycol. Soc.* **51**(3 and 4), 485-92.
- Petch, T. (1925). Additions to Ceylon fungi. III. Ceylon J. Sci. Sec. A. *Ann. R. Bot. Gard. Peradeniya* **9**, 322.
- Reiss, J. (1971). Cytochemical detection of a layer of mucilage around the hyphae of *Cercospora herpotrichoides*. *Trans. Br. Mycol. Soc.* **56**(3), 481-2.
- Saccardo, P. A. (1889). 'Sylloge Fungorum', vol. 8, 905.
- Schröter, J. (1889). Die Pilze Schlesiens. I. Hälfte. In Cohn, 'Kryptogamenflora von Schlesien', vol. 3, 259-60.
- Specht, R. L. (1972). 'The Vegetation of South Australia.' 2nd Ed. (Govt. Printer: Adelaide.)
- Tandy, P. A. (1969). Mycorrhiza in grasses. Hons. Thesis, Univ. of New England.
- Thaxter, R. (1922). A revision of the Endogoneae. *Proc. Am. Acad. Arts Sci.* **57**, 291-350.
- Trappe, J. M., and Gerdemann, J. W. (1972). *Endogone flammicorona* sp. nov., a distinctive segregate from *Endogone lactiflua*. *Trans. Br. Mycol. Soc.* **59**(3), 403-7.
- Tulasne, L. R., and Tulasne, C. (1851). Fungi hypogaei. In 'Histoire et monographie des champignons hypogaei'. (Paris.)
- Warcup, J. H. (1957). Studies on the occurrence and activity of fungi in a wheat-field soil. *Trans. Br. Mycol. Soc.* **40**(2), 237-62.
- Zeller, S. M. (1941). Further notes on fungi. *Mycologia* **33**, 196-214.