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MYCORRHIZAL ENDOGONE SPECIES

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The genus *Endogone* has been amended to include nonsporocarpic types. One new species, *E. mosscae*, with both endocarpic and ectocarpic chlamydospores, and two new varieties with only ectocarpic chlamydospores, *E. macrocarpa* var. *calendonia* and *E. macrocarpa* var. *geospora*, are described. Three new species that form only ectocarpic zygosporic or azygosporic, *E. heterogama*, *E. gigantea* and *E. calospora*, are described. The spores formed by these species have one large suspensor with a much smaller suspensor-like structure projecting from it to the spore. The zygosporic species also produce vesicles on coiled hyphae in soil surrounding plant roots. The three zygosporic species are distinctly different from any previously described species of *Endogone*. All of the species and varieties form endotrophic mycorrhizae.

Three named chlamydosporic species of *Endogone* have been implicated in vesicular-arbuscular mycorrhizae under natural conditions, *E. vesiculifera* Thaxter and *E. fuegiana* Spegazzini (Peyronel, 1924, 1937) and *E. fasciculata* Thaxter (Dowding, 1959). For *E. fasciculata*, this has been confirmed experimentally (Gerdemann, 1965). One zygosporic species, *E. lactiflua* Berk., has been reported to form ectotrophic mycorrhizae on *Pinus strobus* L. (Fassi, 1965). However, there are many other instances where unnamed or unidentified *Endogone* spp. have been noted as mycorrhizal endophytes (Butler, 1939; Mosse, 1956; Gerdemann, 1955, 1961; Nicolson, 1959; Kubíková, 1961; Koch, 1961; Gerdemann and Nicolson, 1963; Meloh, 1963; Mason, 1964; Stevenson, 1964; Ginsberg and Avizohar-Hershenson, 1965; Wastie, 1965.) Most of the fungi described by these authors cannot be assigned to described species of the genus *Endogone* (Thaxter, 1922; Zycha, 1935) and it is apparent that a number of unnamed species are involved. In this paper, the genus *Endogone* is amended to include nonsporocarpic types, four new species are named and described and two varieties are described and placed in the species *E. macrocarpa* (Tul.) Tul.

THE GENUS ENDOGONE

The genus *Endogone* includes zygosporic, chlamydosporic, and sporangial species. Although there is no conclusive evidence for the relationships of these three types (Gerdemann, 1965), because of the general resemblances of spores and sporocarps it is considered desirable to follow Thaxter (1922) in retaining them within one genus.

The sporangial species may be closely related to, or actually belong to, the Mortierellaceae. Kanouse (1936) isolated a zygosporic species, *E. sphagnophila* Atkinson (*E. pisiformis* Link), and in culture it produced chlamydospores, zygospores, and sporangia. The sporangia of this isolate possessed columellae, and since these structures are lacking in the sporangial *Endogone* species she placed them in a new genus *Modicella*, which she assigned to the Mortierellaceae. We believe that this work should be confirmed before the revision is accepted. Walker (1923), who isolated a sporangial species, *E. malleola* Harkness, suggested that this species is closely related to *Mortierella*.

The description of the genus given by Thaxter was modified by Zycha (1935) to include the monotypic genus *Sphaerocreas*. It is proposed here to modify it further to accommodate species and varieties which do not form sporocarps. The inclusion of nonsporocarpic forms within the genus is justified by the fact that *E. microcarpa* Tul. (Godfrey, 1957a) and *E. fasciculata* (Gerdemann, 1965) produce chlamydospores either within sporocarps (endocarpic) or singly on hyphae outside of sporocarps (ectocarpic). The genus description is amended thus.

ENDOGONE Lk. ex Fr. (emend.)

Sporocarps hypogeous or epigeous; containing thick-walled isogamous or heterogamous zygospores with or without specialized envelopes, usually terminal thick-walled chlamydospores or thin-walled sporangia; sporocarps usually containing only one of these types embedded singly or in multiple groups in the sporocarp. Sporocarps naked or surrounded by a variably developed peridium or sometimes covered by a tomentum or hyphal tufts; compact, or loosely coherent, or absent with chlamydospores or zygospores produced singly in soil or in root tissue.

CHLAMYDOSPORIC SPECIES

Endogone mosseae Nicolson & Gerdemann, sp. nov.

FIG. 1.

Sporocarpi plus minusve sphaerici, ad 1 mm diam; peridium varium, ex hyphis septatis irregulariter ramosis in reticulum tenue crebre anastomosantibus efforma-

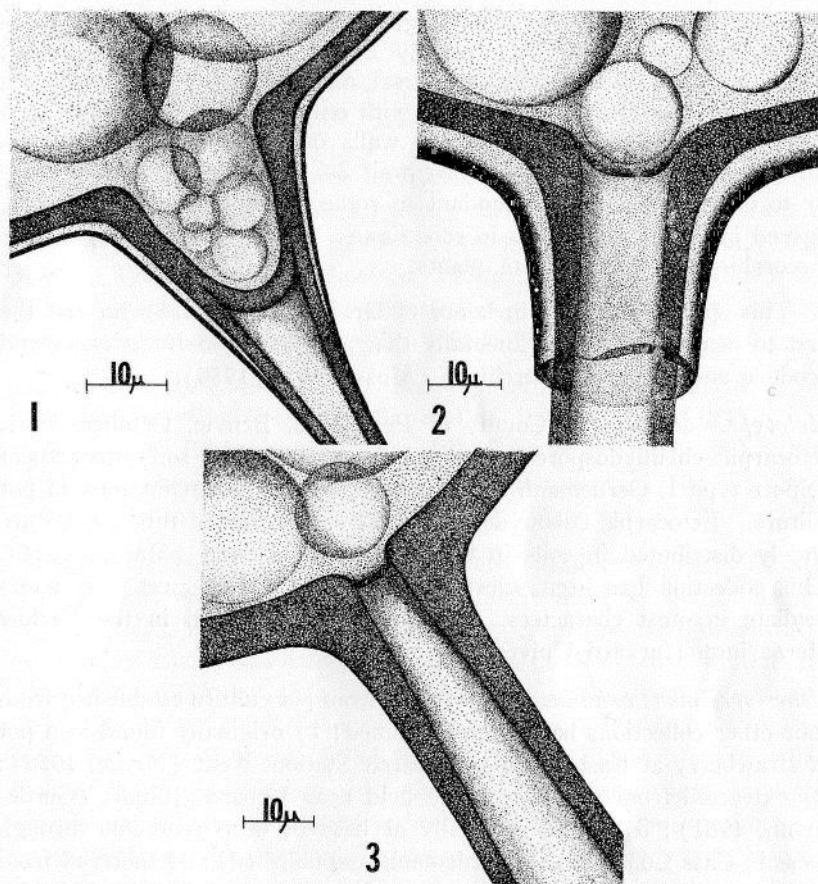


FIG. 1. Base of chlamydospore of *Endogone mosseae*. FIG. 2. Base of chlamydospore of *Endogone macrocarpa* var. *caledonia*. FIG. 3. Base of chlamydospore of *Endogone macrocarpa* var. *geospora*.

tum, chlamydosporas omnino convestiens vel imperfectum, sporas prominere permittens; chlamydosporae plerumque 2-6, nonnumquam ad 32, interdum singulae in sporocarpis productae, luteae, sphaericae vel ovaes, nonnumquam irregulares, magnitudine variae, 60-320 μ diam, plerumque 1-, interdum 2-pedicellatae, pedicello infundibuliformi, tunica duplici, lamina exteriori tenui, interiore crassa, 2-7 μ ; sporaec ectocarpicae similes, quandoque crebrae, quandoque rarae, in humo v. interdum in radicum textu ortae. Mycorrhizam vesiculari-arbuscularem in plantis variis efformat.

Sporocarps more or less spherical, up to 1 mm diam, peridium variable, consisting of irregularly-branched septate hyphae frequently anastomosing to form a thin network, enclosing the chlamydospores entirely,

or incomplete with spores extruding, sporocarps containing chlamydo-spores, sometimes only one, usually 2-6, but up to 32 in number; chlamydospores yellow, spherical to oval, occasionally irregularly-shaped, variable in size 60-320 μ , generally with only one but occasionally two distinct funnel-shaped attachments; walls of spores double with thin outer and thick inner layers, inner wall 2-7 μ ; ectocarpic spores similar to endocarpic spores, abundant in some collections, rare in others, formed in soil or sometimes in root tissue. Forms vesicular-arbuscular mycorrhizae on a variety of plants.

This species is named in honor of Dr. Barbara Mosse who was the first to demonstrate experimentally that a sporocarpic *Endogone* could produce endotrophic mycorrhizae (Mosse, 1953, 1956).

Holotype.—SCOTLAND. County of Perthshire, Benvie, October, 1961, ectocarpic chlamydospores extracted from cultivated soil after wheat (Spore type 1, Gerdemann and Nicolson, 1963) and maintained in pot culture. Ectocarpic chlamydospores and sporocarps of this species are widely distributed in soils in this region of Scotland (Mason, 1964). This collection has been selected as the holotype because it is intermediate in most characters. Type material deposited in the Farlow Herbarium, Harvard University.

Other specimens examined.—Materials from pot culture established from four other collections have been examined: 1) originally found in a pot of strawberry at East Malling Research Station, Kent (Mosse, 1956); 2) extracted from soil in a maize field near Urbana, Illinois (Gerdemann, 1961); 3) found originally at base of deep road cut through loess in Cass Co., Illinois (Gerdemann, unpublished); 4) material from Germany (Koch, 1961).

Most features of this species have been previously illustrated (Mosse, 1956, 1959; Gerdemann, 1961; Koch, 1961; Mason, 1964). All collections produce small sporocarps with a thin peridium of anastomosing hyphae and the spores have the same general appearance. The characteristic funnel-shaped spore attachment (FIG. 1) is of constant occurrence. However, collections differ in spore size, degree of peridial development, and abundance of ectocarpic spores. Since collections overlap with regard to these variable features there does not seem to be any basis for the designation of named varieties. Many spores, particularly endocarpic ones, have two attachments suggesting that they may be zygosporae. However, they resemble typical chlamydospores in other respects, and were regarded as chlamydospores by Godfrey (1957a).

Chlamydospores of this species germinate by emergence of a germ tube from the broken end of an attached hypha. Considerable hyphal growth was obtained by plating surface-sterilized spores on agar media (Mosse, 1959); however, the fungus could not be maintained in pure culture.

A number of studies have been conducted to determine the effects which this species has on plant growth. In general, most authors have obtained an increase in growth (Mosse, 1957; Gerdemann, 1964; Holevas, 1966; Daft and Nicolson, 1966; Murdoch et al. 1967). A decrease in plant growth was reported in mycorrhizal plants infected with the German collection of this species (Meloh, 1963).

ENDOZONE MACROCARPA (Tul.) Tul. Fungi hypog. p. 182. 1851.

Glomus macrocarpus Tul. Giorn. Bot. Ital. I 2: 63. 1845.

E. australis Berkeley. Hooker, Bot. of Antarct. Voy. 3: 282. 1860.

E. pampaloniensis Baccarini. N. Giorn. Bot. Ital. II 10: 79. 1903.

E. tenebrosa Thaxter. Proc. Amer. Ac. Arts Sci. 57: 314. 1922.

Endogone macrocarpa is an extremely variable species. Thaxter (1922) states that it is the most variable member of the genus and suggests that "more than one species may emerge from this rather too comprehensive assortment." Godfrey (1957a) also noted the extreme variability but concluded that because of the existence of intermediate types no subdivision of the species was justified. We have examined some of the material in the Farlow Herbarium on which Thaxter based his revision of the family Endogonaceae and have also been impressed by the extensive variation between the specimens of *E. macrocarpa*. In particular, spore size is a feature which is more variable even than Thaxter indicated. The largest spore diameter he gave for the species was 230 μ . However, in four of the specimens we examined the maximum size exceeded 230 μ , and in one specimen (No. 5218 collected in Tasmania) chlamydospores up to 350 μ were noted.

In this paper *Endogone tenebrosa* Thaxter has been included as a synonym of *E. macrocarpa*. Thaxter described this species from only two preserved specimens, which he records as being in poor condition. A reexamination of the type material suggests that these specimens were old and partially disintegrated when collected and they are overgrown with a contaminating fungus. The species differs from *E. macrocarpa* primarily in the spongy nature of the sporocarp and in the darker color of the chlamydospores. Both these characters could have been due to the state of the specimens and hence there is little basis for retaining *E. tenebrosa* as a separate species.

Two types of spores obtained from cultivated soils and designated *spore types 2 and 3* were found to form typical vesicular-arbuscular mycorrhizae (Gerdemann and Nicolson, 1963). Since 1962 they have been maintained in pot culture on a variety of hosts. They have frequently been reextracted from soil and no intermediate forms have been found either in field soils or in pot cultures. Although the two types have been grown with different hosts, under a variety of conditions, they have never been observed to produce sporocarps. The only structure formed is the chlamydsore. Among named species of *Endogone* the spore types resemble most closely those of *E. macrocarpa* and we propose that they be considered as two named varieties of this species.

Endogone macrocarpa (Tul.) Tul. var. **caledonia** Nicolson & Gerdemann, var. nov. FIG. 2

Chlamydsorae singulatim in humo efformatae, sordide luteae, plerumque sphaericae, nonnumquam ellipsoideae v. irregulares, magnitudine variae, 124–274–391 μ diam, tunica duplaci, laminis distinctis, exteriore tenui, hyalina, 2 μ crass., facile separabili, hypham basalem tegente, collarem efformante, interiore 4 μ crass., lutea, hypham basalem breviter penetrante, pedicello uno haud dilatato, plasmate sporae ab pedicello paulo sub basi ab obturamento separato. Mycorrhizam vesiculari-arbuscularem efformat.

Chlamydsopores formed singly in soil, dull yellow, generally spherical but sometimes ellipsoidal or irregular, variable in size, 124–391 μ in diam with average of 274 μ ; wall consisting of two distinct layers, a thin colorless outer layer 2 μ and thick inner yellow layer 4 μ , outer layer easily removed, and extending along the attached hypha forming a collar, thick inner wall extending into the attached hypha a short distance; single hyphal attachment, not significantly increasing in diameter at base of spore; spore contents separated by basal plug just below point of attachment. Forms vesicular-arbuscular mycorrhizae.

Holotype.—SCOTLAND. County of Perthshire, Mill Hill, October, 1961. Chlamydsopores extracted from pasture soil (Spore type 2, Gerdemann and Nicolson, 1963, FIG. 1) and maintained in pot culture. Ectocarpic chlamydsopores widely distributed in this region of Scotland. Type material deposited in the Farlow Herbarium, Harvard University.

Endogone macrocarpa (Tul.) Tul. var. **geospora** Nicolson & Gerdemann, var. nov. FIG. 3

Chlamydsorae singulatim in humo atque radicibus moribundis efformatae, distincte brunneae, plerumque sphaericae, nonnumquam ellipsoideae, senescentes atrae, magnitudine variabiles, 91–198–318 μ diam, tunica specie simplici, 6–12 μ crass, pedicello uno haud dilatato, tunica crassa hypham basalem longe tegente,

plasmate sporae ab hypha basali prope sporae basim ab abtumento separato. Mycorrhizam vesiculari-arbuscularem efformat.

Chlamydospores formed singly in soil and in moribund roots, distinctly brown, generally spherical but sometimes ellipsoidal, becoming black with age, variable in size, .91–318 μ diam, with an average of 198 μ ; wall with only a single layer detectable, 6–12 μ ; single hyphal attachment not significantly increasing in diameter at base of spore, with thick wall extending into attached hypha for some distance, spore contents separated from hypha by plug near base of spore. Forms vesicular-arbuscular mycorrhizae.

Holotype—SCOTLAND. County of Perthshire, East Newton, October, 1961. Chlamydospores extracted from soil after barley (Spore type 3, Gerdemann and Nicolson, 1963, FIG. 2) and maintained in pot culture. Ectocarpic chlamydospores widely distributed in this region of Scotland. Material of the type has been deposited in the Farlow Herbarium, Harvard University.

Spores produced by *E. macrocarpa* var. *caledonia* are the commonest and largest which occur in many soils in eastern Scotland. The var. *geospora* is also widespread in this region but does not occur in such large numbers as var. *caledonia*. Both varieties have been found under certain conditions to stimulate markedly plant growth (Daft and Nicolson, 1966).

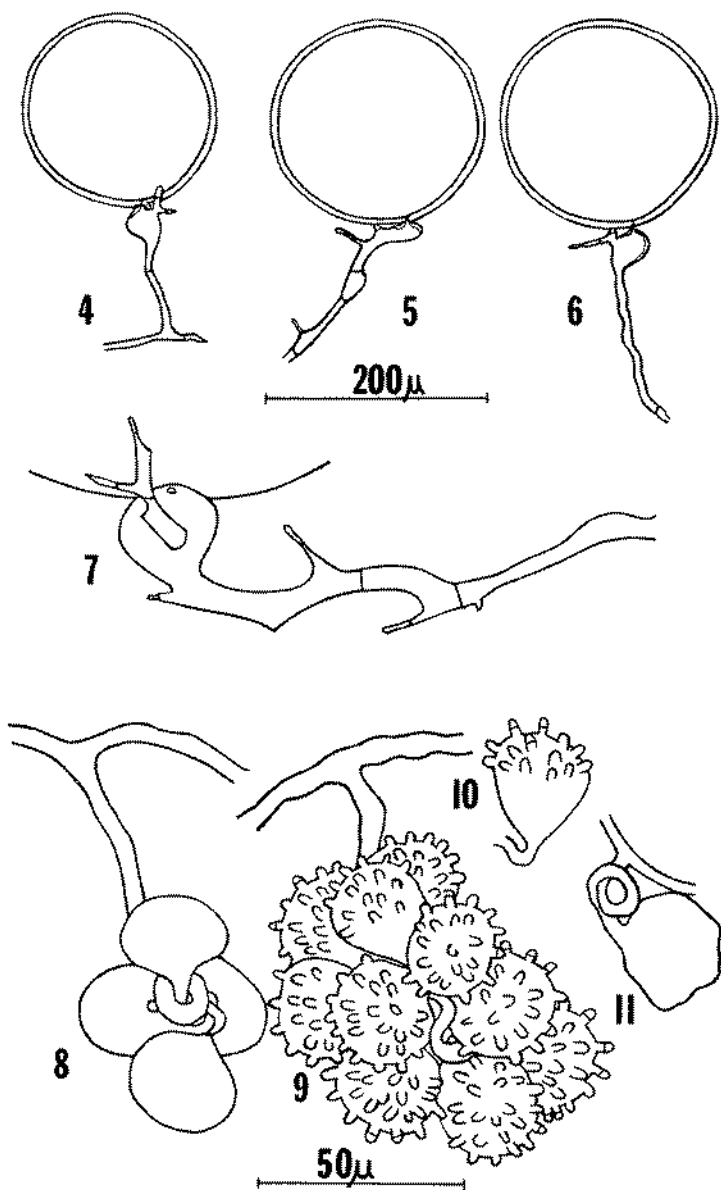
ZYGOSPORIC SPECIES

In addition to *Endogone* chlamydospores, a different type of spore with a bulbous hyphal attachment has also been recorded from soil (Gerdemann 1955, Gerdemann and Nicolson, 1963). These spores are different in several important respects from typical chlamydospores formed by other *Endogone* species and are best regarded as zygospores or azygospores. They have a continuous endospore wall with the opening occluded, a large suspensor with a smaller suspensor-like structure emerging from it, and spore contents which are denser. In contrast to typical *Endogone* chlamydospores, which always germinate by producing a germ tube from the end of the broken hyphal attachment (Godfrey, 1957b), these spores produce a number of germ tubes directly through the spore wall near the attachment.

Three new zygosporic species are described:

Endogone heterogama Nicolson & Gerdemann, sp. nov. FIGS. 4, 5, 6, 7, 8

Zygosporae singulatim in humo v. interdum in radicibus efformatae, pallide brunneae, plerumque sphaericae, 150–202 μ diam, nonnumquam ellipsoideales, ad



FIGS. 4-11. Zygosporic species of *Endogone*. 4-6. Zygospores produced by *E. heterogama*. 7. Base of zygospore of *E. heterogama*. 8. Vesicles formed by *E. heterogama*. 9. Cluster of echinulate vesicles formed by *E. gigantea*. 10. Single vesicle produced by *E. gigantea*. 11. Vesicle formed by *E. calospora*.

253 × 176 μ . v. irregulares, tunica 2–6 μ crass., continua, haud ad instar infundibuli in basim protrusa, canaliculo basali occluso, plasmate ab membrano interiore circumdate, suspensori uno bulbaceo, v. nonnumquam duplici, 21–26 μ diam, lateri affixae, ab hypha gracili e suspensore orta cum eo connexae; tubis germinationis prope basim tunicam penetrantibus; vesiculae sphaericae v. paulo applanatae, brunneae, 16–27 × 20–31 μ singulatim v. in fasciculis duarum ad decem in hyphis complexis ortae in humo efformatae. Efficit mycorrhizam endotrophicam arbusculis praeditam, sed intra radices vesiculis carentem.

Zygospores formed singly in soil, occasionally in roots, light brown, usually spherical, sometimes ellipsoidal or irregular, spherical specimens from 150–202 μ in diam, ellipsoidal specimens up to 253 × 176 μ ; spore wall 2–6 μ , continuous, opening occluded, an inner membrane enclosing spore contents; usually one, occasionally two bulbous suspensors 21–26 μ in diam with a slender hypha extending from the suspensor to the base of the spore, spore attached to the suspensor somewhat laterally; germ tubes produced directly through the spore wall near the base. Spherical to slightly flattened brown vesicles formed in soil, 16–27 × 20–31 μ , in clusters of 1–10 on complex system of intercoiled hyphae. Causes endotrophic mycorrhizae with arbuscules; vesicles lacking in roots.

Holotype.—ILLINOIS, Champaign County, University of Illinois Morrow Plots, continuous maize since 1879, November, 1966. Type material deposited in the Farlow Herbarium.

Not previously recorded. Only known from type locality.

Endogone gigantea Nicolson & Gerdemann, sp. nov. FIGS. 9, 10

Zygosporae singulatim in humo efformatae, maturae vivide luteae colore viridi tinctae, sphaericae, ellipsoideae, cylindricae, v. irregulares, 183–500 × 291–812 μ , tunica exteriore tenui arcte tunicam interiorem 2.5–7.5 μ crassam continuam amplectente, suspensori bulbaceo uno 41–51 μ diam ab hypha gracili cum spora connexo, tubis germinationis tunicam prope basim penetrantibus; vesiculae sphaericae v. clavatae circum apicem septato-echinulatae 22–37 × 20–34 μ singulatim v. in fasciculis duarum ad 16 in hyphis complexis ortae in humo efformatae. Efficit mycorrhizam endotrophicam arbusculis praeditam, sed intra radices vesiculis carentem.

Zygospores formed singly in soil, when mature bright yellow with a greenish tinge, spherical, ellipsoidal, cylindrical or irregular, 183–500 × 291–812 μ , with thin outer wall tightly covering a thick-walled continuous endospore, endospore wall 2.5–7.5 μ ; a single bulbous suspensor 41–51 μ diam with a slender hypha extending from the suspensor to the base of the spore; germ tubes produced directly through the spore wall in the base region. Spherical to clavate vesicles formed in soil, 22–37 × 20–34 μ , in clusters of 1–16 on complex system of

intercoiled hyphae, septate echinulations at apex of vesicles. Causes endotrophic mycorrhizae with arbuscules; vesicles lacking in roots.

Holotype.—ILLINOIS, Champaign County. University of Illinois Morrow Plots, continuous maize since 1879. November 1966. Type material has been deposited in the Farlow Herbarium.

This species is widely distributed in cultivated soils in Illinois. It has also been found in southern Indiana (Clark, unpublished) and in South Dakota (Ohms, 1956). The zygospores (B spores) and vesicles (C spores) have been previously described and illustrated (Gerdemann, 1955). The spores of this species may be the largest produced by any fungus.

***Endogone calospora* Nicolson & Gerdemann, sp. nov.**

FIG. 11

Zygosporeae singulatim in humo v. interdum in radicibus efformatae, hyalinae v. pallide luteae, sphaericae, ellipsoideae, v. cylindricae, magnit. valde variabiles, 126×90 ad $111 \times 511 \mu$, tunica exteriori continua, $3-4 \mu$ crass., membrano interiore tenui, canaliculo ocluso, suspensore bulbaceo, $23-42 \mu$ diam, frequenter hypham gracilem brevem emittente, tubis germinationis tunicam prope basim penetrantibus; vesiculae irregulares, verrucosae, $18-31 \times 22-33 \mu$, singulatim e hypha conspirata in humo efformatae. Efficit mycorrhizam endotrophicam arbusculis praeditam, sed intra radices vesicules carentem.

Zygospores formed singly in soil, occasionally in roots, colorless or light yellow, spherical, ellipsoidal, or cylindrical, dimensions highly variable from a minimum of 126×90 to a maximum of $111 \times 511 \mu$, with an outer wall $3-4 \mu$ and thin inner membrane, spore wall continuous, opening occluded; bulbous suspensor $23-42 \mu$ in diam, often with a slender short hypha projecting from it; germ tubes produced directly through the spore wall in the base region. Irregular vesicles $18-31 \times 22-33 \mu$ formed singly on a coiled hypha in soil. Causes endotrophic mycorrhizae with arbuscules; vesicles lacking in roots.

Holotype.—SCOTLAND. County of Perthshire, East Newton. Cultivated soil, December, 1966. Type material has been deposited in the Farlow Herbarium, Harvard University.

This species is widely distributed in soils of Eastern Scotland, and it has also been noted in soil from one site near Urbana, Illinois. The zygospores have been previously illustrated (Gerdemann and Nicolson, 1963, Spore Type 5).

DISCUSSION

Of the new mycorrhizal species and varieties of *Endogone* described here the chlamydosporic types are similar to those previously described. The zygosporic species, however, are quite different from any species

that has been placed in *Endogone*, and several problems of interpretation arise. The three new species form zygospores which are much larger than those of previously named zygosporic species of *Endogone*, and they are formed singly in soil rather than in sporocarps. Also, in contrast to previously described species where the zygospores are borne on two well-defined isogamous or heterogamous suspensors, spores of the new species normally have only one large suspensor with a slender hypha projecting from it to the spore. Although this hypha is closely appressed to the spore it does not appear to be fused to it. It closely resembles the smaller of the suspensors produced by species of *Zygorhynchus* (Hesseltine et al., 1959) and *Dicranophora fulva* Schroeter. These three new zygosporic species may possess a highly advanced state of heterogamy where the smaller suspensor may be nonfunctional. It is always present in *E. heterogama* and *E. gigantea*, and is especially apparent in *E. heterogama*. In the third species, *E. calospora*, it normally consists of a short projecting tube that usually does not reach to the spore and is often completely absent. Hence, these three species may represent a series in which the smaller gametangium and suspensor are progressively reduced.

Two of the new zygosporic species produce clusters of vesicles in the soil on complex intercoiled hyphae, whereas the third species, *E. calospora*, produces only a single vesicle on a coiled hypha (Figs. 8, 9, 10, 11). They resemble the vesicles produced by *E. vesiculifera*. The vesicles remain thin-walled and are seldom cut off from the attached hyphae by septa. They are filled with oil droplets and sporangiospores have never been observed in them. Vesicles of *E. gigantea* collected from the field late in autumn after the zygospores have matured are empty and collapsed, and it is possible that vesicles of this type may be modified sporangia that function as temporary food reservoirs. In another member of the Mucorales, *Chlamydomucor oryzae* Went & Prinsen, sporangia are produced in which the spores fail to develop.

The three new zygosporic species are distinctly different from all previously described Endogones and it might seem appropriate to place them in a new genus. However, with the current state of our knowledge we do not feel this can be justified. There is a strong possibility that the genus *Endogone* contains several unrelated elements and eventually it may require further revision.

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