

MYCOLOGIA MEMOIR NO. 5

*The Endogonaceae in the  
Pacific Northwest*

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“ . . . la nature franchit de toutes  
parts les limites que nous lui  
marquons si gratuitement. . . .”  
Lamarck 1797

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# THE ENDOGONACEAE IN THE PACIFIC NORTHWEST

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## INTRODUCTION

The Endogonaceae have always presented difficult taxonomic problems. Many early investigators assumed that the large globose zygospores, chlamydospores, or sporangia were asci and placed the family in the Ascomycetes. The classic studies of Bucholtz (1912) on sexual reproduction indicated that the family belonged to the Mucorales. Thaxter (1922), in his monograph of the family, carefully delimited all species known at that time.

A major barrier to a better understanding of the Endogonaceae has been the infrequency of their collection. The discovery that some species produce endomycorrhizae of the vesicular-arbuscular type has greatly stimulated interest in the family, and the development of techniques for extraction of spores from soil has led to the realization that such species are among the most common of all soil-borne fungi (Gerdemann, 1971).

Yet, many questions remain unanswered. It is uncertain if these fungi can be grown in axenic culture. The few reports of successful culture need to be verified. Many species are still rarely collected, and some are known only from the type collection. The complete life cycles of most species are still in doubt. A number of diverse elements are included in the Endogonaceae and quite possibly certain groups of species will eventually be transferred to other families.

The Endogonaceae are particularly well represented in the Pacific



Northwest, and an outstanding collection of specimens has resulted from the many forays of J. M. Trappe and Iwan Ho. Collections of Endogonaceae made in this region by a number of other mycologists were also made available to us.

These studies have resulted in a division of *Endogone* sensu lato, the largest and most heterogeneous genus in the family, into four genera. We do not regard this as a final solution to the taxonomy of the family. We hope that with related species grouped into genera, the Endogonaceae will appear less confusing and that further research thereby will be stimulated.

Our studies of Northwest collections have also resulted in the description of one additional new genus (*Acaulospora*) and 12 new species. New information concerning morphology and geographic distribution was obtained for many previously described taxa.

## MATERIALS AND METHODS

### *Area of Coverage*

The collections on which this paper is based are from central California north to Alaska and east to Idaho. Most of our personal collecting has been in western Oregon. The proportions of collections recorded for a given county or state are directly related to the intensity of sampling. They should not be interpreted as being necessarily meaningful in terms of distribution, relative abundance, or ecological amplitude of a taxon. Such information can be obtained only through a sustained, long-term collecting program that covers all parts of the region adequately.

### *Specimen Collection*

A few Endogonaceae produce epigeous sporocarps and are collected from the tips of moss gametophytes, the surface of soil, litter, wood, or decaying hymenomycetes. However, most species fruit hypogeously, and special techniques are necessary to find them. Species with large sporocarps are collected more or less by chance by raking and searching through the leaf litter and the upper layer of soil. However, with experience a "hypogeous instinct" develops and one learns to dig in likely places.

Species that produce small sporocarps or form spores free in the soil can be collected by wet-sieving and decanting (Gerdemann and Nicolson, 1963). However, the collection of spores and small sporocarps has proven particularly difficult for forest soils. Apparently spores of Endogonaceae are not as common in forest soils as in fields planted to

agronomic or horticultural crops. In addition, most forest soils in the Northwest contain much organic matter, which makes wet-sieving extremely difficult or impossible. Under these conditions, a modification of methods used by Gerdemann (1961) and Gilmore (1968) has proven useful. We term it the "inoculated pot culture" method. Roots and adjacent soil are collected from the endomycorrhizal host plant to be examined. The roots plus particles in 147 to 833  $\mu$  size range (wet-sieved from the sample) are used to inoculate test plants such as *Zea*, *Allium*, or *Lycopersicon* species grown from seed in an autoclaved sandy soil in the greenhouse. Test plants are similarly grown without inoculation for each batch of autoclaved soil as controls to verify that all Endogonaceae in the original soil have been killed. After 3 to 4 months, small cores of soil can be extracted to determine if new spores have matured among the roots. If not, the test plant can be left to grow or senesce until spores are detected by subsequent core sampling. Wet-sieving and decanting can then be used to extract spores or sporocarps and species can be separated under a dissecting microscope.

A useful alternative to inoculated pot cultures for sampling habitats or relatively small plants is the "transplant pot culture" method. Endomycorrhizal plants are dug up in the field and transplanted into pots of autoclaved sandy soil after their roots are washed and freed of debris and extraneous roots. Again, control plants of *Zea* or other species are grown from seed in other pots with soil from the same autoclaving batch as controls. Sampling and spore retrieval are then the same as for the inoculated pot cultures.

#### *Herbarium Deposits*

Sporocarps larger than about 1 mm diam were dried and packeted. Smaller sporocarps and ectocarpic spores and mycelia were put in small, screw-cap vials half-filled with FAA or lactophenol or mounted in lactophenol on microscope slides with the cover glass edge-sealed.

All our collections were assigned Trappe collection numbers and deposited in the Oregon State University Herbarium (OSC). Collections were also examined by loan from these herbaria: Botanisches Institut der Universität, Bern (BERN); Botanical Department of the Hungarian Natural History Museum (BP); National Fungus Collections (BPI); Jardin Botanique National de Belgique (BR); Botanical Museum, University of Copenhagen (C); Central Washington State College (CWSC); Farlow, Harvard (FH); Botanical Museum, Helsinki (H); University of Tasmania (HO); Kew (K); University of Michigan (MICH); New York Botanical Garden (NY); Auckland Plant Disease Division (PDD); University of British Columbia (UBC); and University of California at Berkeley (UC).

### *Microscopy*

Unless otherwise stated, all microscopic examinations were made with mounts in lactophenol. Lactophenol cotton blue is useful for emphasizing hyphal characteristics and for interpreting some types of apparent surface ornamentation of spores. Generally, a KOH solution should not be used as a mounting medium for Endogonaceae, as it causes extreme swelling of some spore walls with a resulting distortion of spores (Gerdemann and Trappe, 1970). However, 5% KOH is useful for certain purposes, e.g. revival of collapsed, thin-walled structures such as gametangia and vesicles. No amyloid reactions have been observed in Melzer's reagent for the Endogonaceae. Melzer's reagent is particularly useful, however, in study of the zygosporic species: the oil globules that often obscure mounts of these taxa in lactophenol or KOH are mostly dissolved; the thickened walls of hyphae that mantle mature zygospores become deep orange; and the spore and gametangial walls of well-preserved, young specimens often become reddish brown (dextrinoid?) in contrast to the nonreactive hyphae of the sporocarp.

### *Problems in Interpretation of Spore Morphology*

Chlamydospores that are formed in contact with soil develop certain features that are likely caused by the action of soil-borne microorganisms. Small perforations often develop within walls, particularly in certain *Glomus* and *Sclerocystis* species. Cylindrical projections sometimes develop from the inner wall at the sites of these perforations, which are continuous through the wall and the projection (Mosse and Bowen, 1968a). Godfrey (1957b) has related these structures to parasitic fungal infections of the spores. Spores filled with apparently parasitic hyphae have been reported for several species of Endogonaceae (Thaxter, 1922; Godfrey, 1957b; Gilmore, 1968), and we have occasionally noted the phenomenon in our collections.

Also, older spores in direct contact with soil often develop a diffuse, granular outer layer. We believe that this results from the digestive action of microorganisms, possibly actinomycetes, on the spore wall. Occasional collections of chlamydosporic species are encrusted with dense bacterial colonies which can be mistaken for a warty surface ornamentation of spores or hyphae. Obviously, great care is required in interpreting surface features of spores in the Endogonaceae. Also, spore walls may darken with age. This is particularly true for specimens stored in lactophenol.

### *Mycorrhiza Formation*

The ability of species of Endogonaceae to form mycorrhizae with specific hosts was either determined experimentally or hypothesized from

association of sporocarps or spores with roots. Experimental determination entailed inoculation of plants grown in autoclaved soil with field-collected spores or sporocarps. The inoculum was carefully selected to assure that only one species of Endogonaceae was present. To confirm mycorrhizal infection of test plants, roots were washed, cleared and stained by autoclaving in acid fuchsin dissolved in lactophenol or chloral hydrate, and destained by boiling in lactophenol alone.

Presumptive mycorrhizal associations were hypothesized either from the fungi that sporulated in single-host transplant pot cultures or by association of a fungus with roots of specific plants sampled in the field or greenhouse. In both cases, great care is needed to insure that roots of extraneous, nearby hosts are not intermingled with the host being examined.

## GENERA AND SPECIES OF ENDOGONACEAE

### *Generic Taxonomy*

Thaxter (1922) recognized four genera in the Endogonaceae: *Endogone*, *Sphaerocreas*, *Sclerocystis*, and *Glaziella*. Zycha (1935) transferred the one species of *Sphaerocreas* recognized by Thaxter to *Endogone*.

The genus *Endogone* as recognized by Thaxter (1922), Zycha (1935), Nicolson and Gerdemann (1968), and Zycha et al. (1969) consists of several diverse elements that may not be closely related. The genus thus constituted is so broad that generalizations concerning it are nearly impossible. Also, the assumption of a close relationship among such diverse elements is apt to lead to unwarranted conclusions concerning phylogeny of the Endogonaceae. Therefore we have divided *Endogone* sensu lato into four genera, recognizing three genera that were previously described but which have been placed in *Endogone* by recent authors, and describing one new genus. The four genera include *Endogone* (Link, 1809), sporocarpic with zygospores formed above the point of union of two gametangia or budding from the larger of the two, at least one species ectomycorrhizal; *Glomus* (Tulasne and Tulasne, 1845), sporocarpic or nonsporocarpic with chlamydospores generally formed terminally on a single undifferentiated hypha, most, if not all, species will probably prove to be endomycorrhizal; *Gigaspora* (described herein), nonsporocarpic with azygospores (?) borne on a large suspensor, all known species endomycorrhizal; and *Modicella* (Kanouse, 1936), sporocarpic with thin-walled sporangia, mycorrhizal relationships unknown.

We have described an additional new genus, *Acaulospora*, for two species previously undescribed. It is nonsporocarpic with azygospores (?) borne singly and laterally on a hypha which terminates

nearby in a large thin-walled vesicle. *Acaulospora* species form endomycorrhizae resembling those produced by *Glomus*.

Chlamydosporic species (*Glomus*) and sporangial species (*Modiella*) have generally been assumed to represent asexual stages of zygosporic species (*Endogone*). However, there is little evidence that this is true; assumption of such relationships can lead to unwarranted conclusions. For example, the sporangial species lack columellae, and this has been cited as evidence for a relationship of all Endogonaceae to the Mortierellaceae. There is, however, almost no evidence that sporangial species are related to other Endogonaceae, and they may in fact belong to the Mortierellaceae (Walker, 1923; Kanouse, 1936).

The production of zygospores in sporocarps by *Endogone* spp. has also been used as evidence for a relationship of the Endogonaceae to the Mortierellaceae, a few species of which produce a hyphal mantle around the zygospores. However, zygospores in the two families form in distinctly different ways. In the Mortierellaceae the zygospore forms within the space occupied by the two gametangia, while in *Endogone* the zygospore buds out from the point of union of the two gametangia or from the larger to form an external zygospore (*E. stratosa* described in this paper and *E. multiplex* Thaxter may be exceptions: in both species the attachments on mature spores are separated from each other, but in neither case have young stages been available to determine the manner in which spores form). In *Endogone* zygospore formation is similar to that of *Piptocephalis* and *Syncephalis* in the Piptocephalidaceae (Benjamin, 1959), and perhaps this is where one should look for relationships. The failure of *Endogone* zygospores to germinate under experimental conditions is a major barrier to a better understanding of this genus.

The zygospores of *Endogone* and the chlamydospores of *Glomus* superficially resemble each other (see discussion of *Endogone* following the key to genera), and sporocarps of the two genera are so similar that a microscopic examination is generally necessary to distinguish them. The existence of two sporocarps containing both chlamydospores and zygospores is the only real evidence for a relationship of the two genera (Thaxter, 1922; Godfrey, 1957a). However, in both sporocarps the hyphae associated with the two types of spores are unlike (Gerdemann, 1965, and present paper under *Glomus*), and it is possible that these sporocarps consist of chance mixtures of two species. Also the possibility of hyperparasitism cannot be dismissed.

Numerous *Glomus* species have been maintained in "pot culture" on roots of living plants for long periods. Under these conditions they have never formed zygospores. The ecology of *Glomus* appears to differ from that of *Endogone*. Many *Glomus* species are known to form endomycorrhizae, and in nature they are usually associated with endomycorrhizal hosts. *Endogone* species, on the other hand, tend to be associated with

ectomycorrhizal plants; Fassi and Palenzona (1969) have experimental evidence that one species forms ectomycorrhizae.

*Gigaspora* species were first described and placed in *Endogone* by Nicolson and Gerdemann (1968). However, they recognized that this group of species did not closely resemble other members of the genus and indicated that, if *Endogone* were to be revised, such species would probably be placed in a new genus.

The spores formed by *Gigaspora* species in some respects resemble *Endogone* zygospores. However, they form in a distinctly different way: Each is borne at the tip of a single large suspensor-like cell from which a slender hypha usually projects to the spore. However, there is no obvious sexual fusion, and perhaps such spores are best regarded as azygospores. The one large suspensor-like cell is suggestive of *Zygorhynchus* (Hesseltine et al., 1959) and certain *Mortierella* species (Gams and Williams, 1963; Kuhlman, E. G., personal communication). However, sporangia that would relate *Gigaspora* to either *Zygorhynchus* or *Mortierella* have not been observed. *Gigaspora* species produce distinctive soil-borne vesicles which, in some cases, suggest the terminal heads of merosporangiophores produced by certain species of Piptocephalidaceae. All known species form endomycorrhizae similar to those produced by *Glomus* species.

*Sclerocystis* is very closely related to *Glomus*, differing from it only in the orderly arrangement of chamydospores within the sporocarp. In *Sclerocystis* the spores are tightly arranged in a single layer surrounding a central plexus of sterile hyphae. *Sclerocystis* species produce endomycorrhizae indistinguishable from those formed by certain *Glomus* species.

*Glaziella* is also very closely related to *Glomus*, differing from it in that the chlamydospores are borne within the walls of large hollow sporocarps. It is known only from tropical lowlands and has never been collected in the Northwest. Its mycorrhizal relationships are unknown.

## ENDOGENACEAE

### KEY TO GENERA

1. Chlamydospores or sporocarpic sporangia, borne terminally on persistent, undifferentiated hyphae ..... 4
1. Zygospores or azygospores, borne terminally on gametangia, or suspensors (?), or on a single, bulbous, suspensor-like cell, or laterally on a broad hypha that terminates nearby in a large vesicle (spore bearing cells often disappearing by maturity, so spores often lacking an attachment) ..... 2
  2. Zygospores borne in sporocarps; two gametangia, or suspensors (?), evident in young specimens, but generally by maturity no hyphal attachments perceptible ..... I. *Endogone*
  2. Azygospores borne free in soil, terminally on a persistent, single suspensor-like cell or laterally on a large, readily collapsing hypha that terminates nearby in a large vesicle ..... 3

3. Azygospores terminal on a single, suspensor-like cell from which a slender hypha generally projects to the spore ..... II. *Gigaspora*
3. Azygospores borne laterally on a large, readily collapsing hypha that terminates nearby in a large vesicle ..... III. *Acaulospora*
4. Thin-walled sporangia, borne in sporocarps ..... VI. *Modicella*
4. Chlamydo­spores borne free in soil or in sporocarps ..... 5
5. Chlamydo­spores borne free in soil or distributed at random or in several rows in solid sporocarps ..... IV. *Glomus*
5. Chlamydo­spores tightly arranged in a single layer around a central plexus of sterile hyphae or borne in the wall of a large, hollow sporocarp ..... 6
6. Sporocarps solid, less than 1 mm diam but often fused in crust-like masses; spores in a single layer around a central plexus of sterile hyphae ..... V. *Sclerocystis*
6. Sporocarps hollow, over 10 mm diam, the wall containing widely spaced chlamydo­spores (extralimital genus) ..... VII. *Glaziella*

**I. ENDOGONE** Link ex Fries, Syst. Mycol. 2: 295. 1823.

*Type species: Endogone pisiformis* Link ex Fr.

Zygospores formed in sporocarps by budding from the tip of the larger of two gametangia, or, if the gametangia equal or subequal, spores generally bud from the top of the point of union. In two species zygospores borne on suspensors (?) separated from each other. Spores randomly distributed in sporocarps or formed in rows radiating from the base.

**ETYMOLOGY:** Greek, *endo-* (inside) and *-gone* (reproductive organs): "with reproductive organs inside."

In the Endogonaceae, sexual reproduction has been definitely established only for this genus (Bucholtz, 1912). Zygospores have been found only in sporocarps, and their germination has never been observed (Godfrey, 1957c). In none of the species that we include in this genus have spores other than zygospores been found in or associated with the sporocarps. Both Thaxter (1922) and Godfrey (1957a) found zygospores associated with a single collection of a chlamydo­sporic species. The zygospores in these two collections are similar; however, they do not appear to belong to a named *Endogone* species, and the material in both collections is inadequate for describing a new species. (See the discussion under *Glomus*.)

Until sporangial stages are found, the relationship of these fungi to other Mucorales will remain obscure. Kanouse (1936) reported obtaining *E. sphagnophila* Atk. (*E. pisiformis*) in pure culture and reported that such cultures produced chlamydo­spores, zygospores, and sporangia with columellae. However, her illustrations of the zygospores formed in culture are atypical for *E. pisiformis*. Also, the chlamydo­spores were intercalary, whereas chlamydo­spores formed by *Glomus* species are generally terminal. Possibly atypical structures are formed in agar cultures; in any event, unless this work can be repeated, we believe that it is open to serious question.

Bakerspigel (1958a) described nuclear structure and division in sporangiospores from a culture of *E. sphagnophila* isolated from dead and dying roots of *Betula lutea* Michx. However, the sporangia were not described and the bases for the identification of the isolate as an *Endogone* species were not given.

We attempted to isolate *E. pisiformis* from freshly collected sporocarps. Small portions of sporocarps were surface sterilized in hydrogen peroxide, rinsed in sterile water and plated on the Marx modification of Melin-Norkrans' culture medium (MMN) (Marx, 1969). Very slow growing yellow isolates were obtained. The hyphae were nonseptate, 2–12.5  $\mu$  in diam, and irregular in shape. Inflated cells were abundant, up to 83 $\mu$  diam, thin-walled, generally intercalary, and at times terminal or forming as a lateral bulge from a hypha. Hyphae and inflated cells contained much yellow oil, similar in color to that in sporocarps of *E. pisiformis*. Zygospores, chlamydospores, and sporangia were not produced.

Isolates also grew on potato dextrose agar but not as well as on MMN. They did not grow on corn meal agar. Since sporulation was not obtained cultures could not be identified. However, we believe that they were probably isolates of *E. pisiformis*.

All *Endogone* species form sporocarps hypogeously except for *E. pisiformis*, *E. incrassata* Thaxter and *E. acrogena* Gerd., Trappe & Hosford, which produce sporocarps that may be either hypogeous or epigeous (*E. flammicorona* Trappe & Gerd. has been found on the soil surface in forest tree nurseries, but its habit in natural stands is hypogeous). Hypogeous sporocarps are generally discovered more or less by accident by raking or digging in the soil, so most *Endogone* spp. are infrequently collected. In the Pacific Northwest, they are usually found in coniferous or mixed coniferous-hardwood forests and are generally associated with ectomycorrhizal hosts. As far as we are aware they have not been collected from grasslands or cultivated soils planted to agronomic or horticultural crops. Also, there do not appear to be any records of their collection in strictly tropical climates [see *E. alba* (Petch) Gerd. & Trappe]. Evidence for a mycorrhizal relationship exists for only one species: *Endogone flammicorona* (formerly designated *E. lactiflua* Berk. & Broome) has been found closely associated with ectomycorrhizae of pines and Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] in an Italian nursery and of Douglas fir in a nursery in Washington (Fassi, 1965; Fassi et al, 1969). Fassi and Palenzona (1969) inoculated Douglas fir and *Pinus strobus* L. seedlings grown from seed in pots of autoclaved soil with surface-sterilized sporocarps. A distinctive type of ectomycorrhiza was formed, and after 2 years *E. flammicorona* fruited anew among the mycorrhizae. Uninoculated control pots were devoid of mycorrhizae. As noted later, *E. pisiformis* frequently fruits on sub-



strates that preclude the possibility of an obligate ectomycorrhizal association.

It is sometimes difficult to distinguish zygosporic from chlamydo-sporic species. Gametangia are generally thin-walled, ephemeral, and are seldom discernible on mature zygospores. Only *E. lactiflua* produces thick-walled gametangia that at times persist on mature spores. Most chlamydo-spores, on the other hand, have a single, persistent hyphal attachment which is easily recognizable. Mature zygospores always have double walls, and the outer wall is usually thickened and not membranous. Chlamydo-spores may have either single or double walls. If they are double, the outer wall is usually thin and membranous. In young zygospores, the outer walls are continuous with the walls of the gametangia. As the spores mature, the gametangia generally disappear, leaving an opening in the outer wall. A continuous inner wall develops that completely occludes this opening. In both zygospores and chlamydo-spores, the walls are often formed from an indefinite number of tightly fused layers. True double walls are generally distinct and easily distinguishable from such laminate walls. The oil globules contained in zygospores are usually smaller and much more uniform in size than those in chlamydo-spores.

#### KEY TO THE SPECIES OF ENDOGONE

- |   |                           |
|---|---------------------------|
| 1. Spores enclosed in a tightly appressed hyphal mantle .....   | 2                         |
| 1. Spores lacking a hyphal mantle .....   | 5                         |
| 2. Spores randomly distributed in rounded sporocarps .....  | 3                         |
| 2. Spores arranged in discreet rounded clusters in rounded sporocarps or formed in thin strata .....  | 4                         |
| 3. Hyphae of spore mantle in two to many layers, frequently branching and intertwined, not spirally arranged; in cross section, the mantle appears netted. Spores usually broader than long .....                 | 1. <i>E. lactiflua</i>    |
| 3. Hyphae of spore mantle mostly in a single layer with a spiral, sinuous pattern; in cross section, hyphal wall thickenings appear as flame-like projections from spores. Spores usually longer than broad ..... | 2. <i>E. flammicorona</i> |
| 4. Sporocarps of smooth to verrucose, folded and convoluted strata .....  | 3. <i>E. stratosa</i>     |
| 4. Sporocarps rounded (extralimital species) .....  | 9. <i>E. multiplex</i>    |
| 5. Spores distributed more or less at random .....  | 6                         |
| 5. Spores formed in discrete rounded clusters or arranged in radiate rows .....   | 9                         |
| 6. Spores borne in greatly convoluted strata incorporating much soil (extralimital species) .....   | 10. <i>E. tuberculosa</i> |
| 6. Spores borne in small compact sporocarps, generally free of soil .....   | 7                         |
| 7. Sporocarps ovoid, to $0.6 \times 1$ mm, fused together in pulvinate masses (extralimital species) .....  | 11. <i>E. alba</i>        |
| 7. Sporocarps generally larger than $0.6 \times 1$ mm, not fused together in masses ....  | 8                         |
| 8. Spores generally not exceeding $75(-83) \mu$ diam, the inner wall thicker than the outer; sporocarp cavity, when present, open at the base .....   | 4. <i>E. pisiformis</i>   |
| 8. Spores often exceeding $90 \mu$ diam, the outer wall thicker than the inner; sporocarp cavity, when present, not opening to the exterior ....  | 5. <i>E. incrassata</i>   |

- 9. Spores formed in radiate rows, with the youngest at the surface of the sporocarp ..... 8. *E. acrogena*
- 9. Spores grouped in discreet, rounded clusters ..... 10
- 10. Spores shorter than 60  $\mu$ ; sporocarp lacking a peridium ..... 6. *E. verrucosa*
- 10. Spores mostly longer than 70  $\mu$ ; sporocarp with a peridium ..... 7. *E. oregonensis*

1. **Endogone lactiflua** Berk. & Broome, Ann. Mag. Nat. Hist. Ser. 1, 18: 81-82. 1846. Non sensu Bucholtz, Beih. Bot. Centbl. 39: 147-224. 1912. FIG. 1

=*Endogone lanata* Harkn., Proc. Calif. Acad. Sci. Ser. 3, 1: 280. 1899.

=*Endogone rosea* Zeller, Mycologia 33: 214. 1941.

Sporocarps 3-9(-15) mm broad, subglobose to ellipsoid or reniform, in occasional collections lobed and irregular, usually with a basal attachment to the soil. Peridium thin, white, partially or completely disappearing in old specimens. Gleba sometimes sterile at base, in youth pale yellow and exuding a sticky latex, later appearing as a rather loosely woven, dry white tissue dotted with brown spores, and finally with the glebal tissue mostly collapsed to leave a brown aggregation of spores. Zygosporcs 71-180  $\times$  94-190  $\mu$ , orange-brown, globose to ellipsoid, usually broader than long. Spore wall 5-11  $\mu$  thick, consisting of a brown outer wall 1-3  $\mu$  that stains deep reddish brown in Melzer's reagent and a thicker, yellow, inner wall. Immature spores embedded in thin-walled vesicular hyphae; as spores mature becoming enclosed in hyphal mantles 5-50  $\mu$  thick, composed of two to many layers of thick-walled, intertwinning, branching and anastomosing hyphae, in cross section appearing netted and fairly readily separating from the outer wall of cut spores. Gametangia large, up to 65(-80)  $\mu$  broad, often becoming thick-walled and persisting, parallel, of unequal size, with the zygosporc budding from the tip of the larger of the two.

DISTRIBUTION, HABITAT, AND SEASON: Hypogeous, widely distributed and rather common in coniferous or *Quercus* forests from sea level to subalpine zones. Generally found from April through July but occasionally as late as November. Also in eastern North America and Europe.

MYCORRHIZAL ASSOCIATIONS: Associated as a probable ectomycorrhiza former with roots of members of the Pinaceae [e.g. *Abies amabilis* (Dougl.) Forbes, *A. lasiocarpa* (Hook.) Nutt., *Picea sitchensis* (Bong.) Carr., *Pinus contorta* Dougl., *Pinus ponderosa* Dougl. ex Loud., *Pseudotsuga menziesii*, and *Tsuga heterophylla* (Raf.) Sarg.] as well as *Quercus garrayana* Dougl.

ETYMOLOGY: Latin, *lacti-* (milk) and *fluo* (flowing), referring to the latex exuded by cut surfaces of fresh, young sporocarps.

COLLECTIONS EXAMINED: ALASKA—Kenai Peninsula, Wells-Kempton 3018 (OSC and Wells-Kempton Herb.). CALIFORNIA—

*Humboldt Co.*: Parks 5763 (UC 62494). *Placer Co.*: Harkness 45b (BPI, holotype of *E. lanata*), Harkness 99 (BPI, as *E. macrocarpa*). *Siskiyou Co.*: W. B. Cooke 13295 (NY), W. B. Cooke 42797 (OSC). OREGON—*Benton Co.*: Trappe 546, 2439, 2620, 2643, 2719 (OSC); Alsea Mountain, April 1939, leg. H. M. Gilkey (NY, type of *E. rosea* Zell., immature); Zeller 8469 (NY). *Coos Co.*: Trappe 2706, 2710, 3207 (OSC). *Curry Co.*: Trappe 2683 (OSC). *Deschutes Co.*: Trappe 3234 (OSC). *Douglas Co.*: Trappe 3004 (OSC). *Josephine Co.*: E. L. Stewart 392 (OSC). *Lane Co.*: Trappe 1705, 2858 (OSC). *Lincoln Co.*: Fogel 465 (OSC). *Linn Co.*: Roaring River Fish Hatchery, 30 April 1938, leg. S. M. Zeller (NY); Zeller 8482 (NY); Trappe 2803 (OSC). *Polk Co.*: Trappe 2454 (OSC). *Tillamook Co.*: Trappe 866, 1976, 2313, 2343, 2359, 2432 (OSC). *Wallowa Co.*: Hat Point, 27 July 1939, leg. A. M. Rogers (NY); Trappe 1917 (OSC). *Yamhill Co.*: Bald Pk. St. Park, 14 June and 22 July 1964, leg. Oswald & Goetz (MICH). WASHINGTON—*Lewis Co.*: Trappe 1871 (OSC). *Pierce Co.*: Mt. Rainier Nat. Park, Hosford 615 (CWSC and OSC).

2. **Endogone flammicorona** Trappe & Gerdemann, Trans. Brit. Mycol. Soc. 59: 403–407. 1972. FIG. 2

= *Endogone lactiflua* sensu Fischer, Bucholtz et auctt. pl.

Sporocarps 3–25 mm broad, mostly globose to subglobose and white when immature, at maturity mostly lobed and convoluted and buff to dull orange-brown with soil particles frequently adhering to surface. Peridium thin, white, becoming buff, often disappearing on mature specimens. Gleba at first white, becoming buff or salmonaceous and finally orange-brown in fully matured specimens, often exuding a sticky latex when cut. Zygospores  $52\text{--}120 \times 42\text{--}99 \mu$ , globose to ellipsoid or obovoid, usually longer than broad, containing oil globules  $2\text{--}3 \mu$  diam; spore wall  $3.5\text{--}7 \mu$  thick, consisting of a thin, deep yellow to brown outer wall  $1\text{--}2 \mu$  that is yellow to pale orange in Melzer's reagent and a thick, hyaline to light yellow inner wall up to  $6 \mu$ . Spores enclosed in a tightly adherent hyphal mantle (Flammenkrone)  $5\text{--}20 \mu$  thick, usually a single layer of hyphae encircling each spore in a spiral, sinuous manner, with lateral walls pressed together; in cross section bases of hyphae (adjacent to spore) and lateral walls greatly thickened, the thickening becoming progressively thinner toward the outer, generally thin-walled hyphal surface, thickened lateral walls of two adjacent hyphae coalesced to form pointed, flame-shaped projections (Flammen) from spore. Gametangia up to  $35$  ( $\text{--}40$ )  $\mu$  broad, thin-walled and ephemeral, not visible on mature spores, parallel, of unequal size, with the zygospore budding from the tip of the larger of the two.

DISTRIBUTION, HABITAT, AND SEASON: Hypogeous or rarely subhypogeous, rare but widely distributed in coniferous forests from coastal areas to relatively low elevations in the mountains and in seedling beds

of a tree nursery. Collected in spring, early summer, fall, and early winter. Widespread but infrequent in North America and Europe.

MYCORRHIZAL ASSOCIATIONS: Occurring among ectomycorrhizae of Pinaceae (e.g. *Pinus radiata* D. Don and *Pseudotsuga menziesii*); a demonstrated ectomycorrhizal fungus (Fassi and Palenzona, 1969).

ETYMOLOGY: Latin, *flammi-* (flame) and *corona* (crown), referring to the flame-shaped projections of the spore mantle as seen in cross section.

COLLECTIONS EXAMINED: CALIFORNIA—*San Francisco Co.*: Sundberg 1348 (OSC). IDAHO—*Bonner Co.*: A. H. Smith 68483 (MICH). OREGON—*Coos Co.*: Trappe 3206 (OSC). *Linn Co.*: Gilkey 446 (OSC). *Polk Co.*: Stewart 340 (OSC); Trappe 2820 (OSC). *Tillamook Co.*: Trappe 2280 (OSC). WASHINGTON—*Pierce Co.*: Hosford 58 (CWSC). *Skamania Co.*: Trappe 506 (OSC and MICH).

*Endogone flammicorona* and *E. lactiflua* differ in the following characters:

<i>E. lactiflua</i>	<i>E. flammicorona</i>
Sporocarps:	
Subglobose to ellipsoid or reniform, rarely lobed or irregular.	Generally lobed and irregular.
Spores:	
Globose to ellipsoid, generally broader than long with a breadth of 94–190 $\mu$ .	Globose, ellipsoid, or obovoid, usually longer than broad with a breadth of 42–99 $\mu$ .
Spore mantles:	
Consisting of several layers of interwoven hyphae, appearing netted in cross-section; readily separating from spore walls.	Generally consisting of a single layer of spirally arranged hyphae, appearing as flame-shaped projections in cross section; adhering tightly to spore walls.
Spore walls:	
Outer wall becomes dark reddish brown in Melzer's reagent.	Outer wall becomes yellow to pale orange in Melzer's reagent.
Gametangia:	
Thick-walled, often persistent, up to 80 $\mu$ broad.	Thin-walled, ephemeral and generally not visible on mature specimens, not broader than 40 $\mu$ .

For further information on these two species see Trappe and Gerdemann (1972).

### 3. *Endogone stratosata* Trappe, Gerdemann & Fogel, sp. nov.

Sporocarpia 1  $\times$  3–6 mm, e stratis laevibus, plicatis convolutisque, vel verrucosis consistentia super solum metallicum vel in eo occurrentia, frequenter cum spororum circulis albis vel griseis, inconspicuis, irregularibus socia. Sporocarpia in soli superficie nata a peridio albo e hyphis intertextis, hyalinis, tenuiter tunicatis, 1.5–4  $\mu$

diametro efformato induta, immersa eo carentes. Hyphae byssiodeae, albae, instar peridii in spatiis inter strati plicas occurrentes. Hyphae glebae hyalinae, tenuiter tunicatae, 3-8  $\mu$  diametro, vesiculis ad 20  $\mu$  diametro inspersae, sporis auctis oppressae. Zygosporae arcte appressae, interdum in circulis subglobosis vel globosis ordinatae, hyalinae, 113-177  $\times$  82-149  $\mu$ , plerumque quam latitudo longiores, globosae, ellipsoideae, ovoideae, obovoideae, pyriformes, vel pressae irregulares, globulos aequos hyalinos oleosos continentes. Sporae tunica e laminibus duobus facile separabilibus, utrisque 4-8  $\mu$  crassis, aequis vel subaequis crassitudine, composita. Sporae a palla arcte adhaerente 8-15  $\mu$  crassa e hyphis hyalinis, crasse tunicatis 2-6  $\mu$  diametro intertextis inclusae. Gametangia (vel suspensores) 35-40  $\mu$  diametro, tenuiter tunicata, prope sporae basim spatio aliquanto inter se separata. Tunica interior anulum efformans ad locum colligationis per porum in exteriori partim protrudens.

Sporocarps 1  $\times$  3-6 mm, consisting of smooth to folded and convoluted, or verrucose strata on or in mineral soil, irregular groups of spores often present in soil adjacent to strata, white to gray, inconspicuous. Sporocarps on soil surface with white peridium of interwoven, hyaline, thin-walled hyphae 1.5-4  $\mu$  diam, lacking on sporocarps embedded in soil. Cottony white, peridium-like hyphae present in cavities between the folds of strata. Glebal hyphae hyaline, thin-walled, 3-8  $\mu$  diam, with vesicles up to 20  $\mu$  diam, becoming crushed as spores enlarge. Zygosporae tightly appressed, at times arranged in subglobose to globose clusters, hyaline, 113-177  $\times$  82-149  $\mu$ , mostly longer than broad, globose, ellipsoid, ovoid, obovoid, pyriform, or irregular from pressure, containing uniformly-sized, hyaline oil globules. Spore wall of 2 readily separable layers, each 4-8  $\mu$  thick, equal or subequal in thickness. Spores enclosed in a tightly adhering mantle 8-15  $\mu$  thick of hyaline, thick-walled, interwoven hyphae 2-6  $\mu$  diam. Gametangia (suspensors?) 35-40  $\mu$  diam, thin-walled, at spore base separated some distance from each other. Inner wall forming a ring which partially protrudes through the opening in the outer wall at points of attachment.

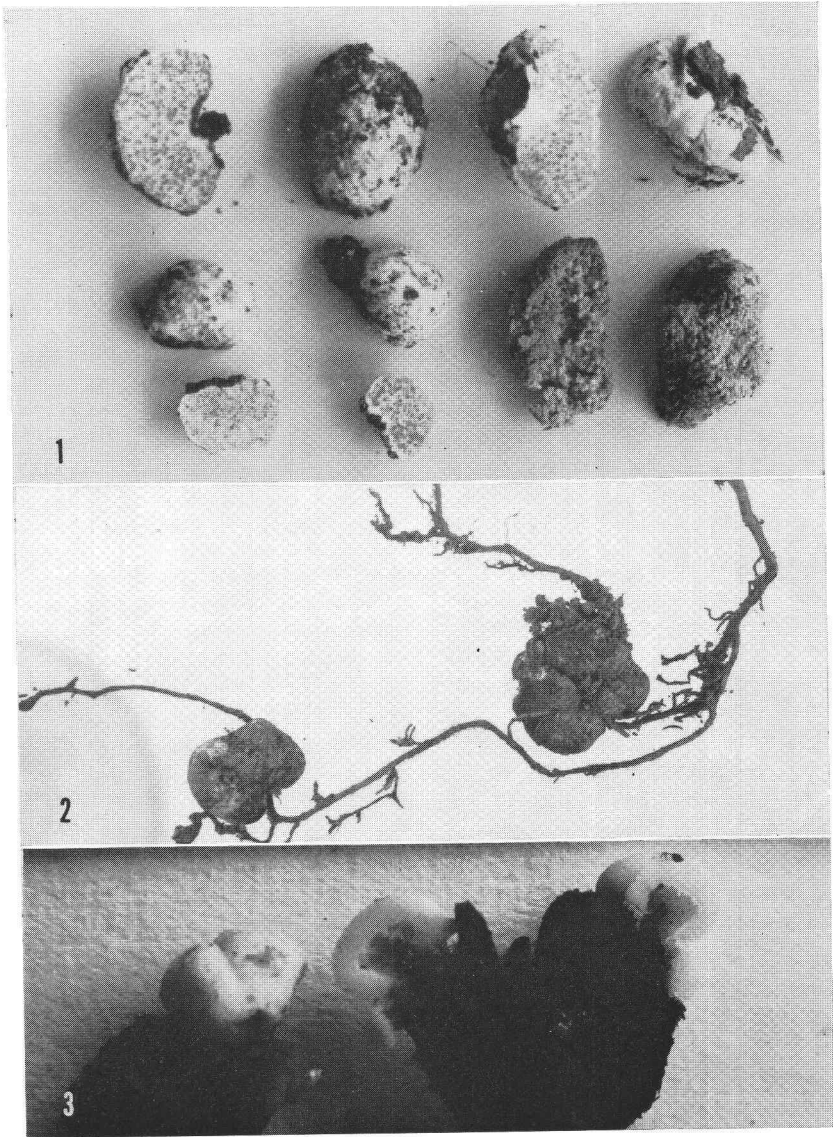
DISTRIBUTION, HABITAT, AND SEASON: On or in mineral soil under humus in a 40-year-old stand of *Pseudotsuga menziesii*; known only from the type collection.

MYCORRHIZAL ASSOCIATIONS: Unknown.

ETYMOLOGY: Latin, *stratosus* (layered), referring to the form of the sporocarp.

COLLECTIONS EXAMINED: TYPE: OREGON—*Benton Co.*: 2 miles east of Bunker Hill (west of Bellfountain), 8 June 1971, R. Fogel 485 (OSC).

*Endogone stratosus* resembles *E. multiplex* Thaxter, a species thus far not encountered in the Pacific Northwest, in having zygosporae borne on two separated attachments (suspensors?) with each individual spore tightly enclosed in a hyphal mantle. However, the spores of *E. stratosus* are arranged at random, or at times in irregular to globose groups, in thin strata, whereas the spores of *E. multiplex* are in coherent globose spore clusters which are aggregated into a rounded sporocarp. In addi-



FIGS. 1-3. Sporocarps of *Endogone*. 1. *Endogone lactiflua*, surface and cross-sectional views,  $\times 3.2$ . 2. *Endogone flammicorona*, attached to roots of *Pseudotsuga menziesii*,  $\times 1.5$ . 3. *Endogone pisiiformis*, surface and cross-sectional views, showing a central cavity with a basal opening,  $\times 4.5$ .

tion, the spores of *E. stratosa* are larger than those of *E. multiplex* ( $48-125 \times 48-91 \mu$ ) in the type specimen.

The separation of spore attachments in *E. stratosa* and *E. multiplex* suggests that their zygospores form in a manner different from other *Endogone* species. Possibly such zygospores develop within gametangia. This puzzle cannot be solved, however, until younger stages are available for study.

4. *Endogone pisiformis* Link ex Fries, Syst. Mycol. 2: 296. 1823.

FIGS. 3, 4

=(?)*Protomyces xylogenus* Sacc., Michelia 1: 14. 1877.

=*Endogone xylogena* (Sacc.) Schroeter, sensu Schroeter, forte non Saccardo in F. Cohn, Kryptogamen-Flora von Schlesien 3 (pt. 1): 260. 1887.

=*Endogone ludwigii* Bucholtz, Beih. Bot. Centbl. 29: 194. 1912.

=*Endogone sphagnophila* Atkinson, Brooklyn Bot. Gard. Mem. 1: 16. 1918.

=*Endogone occidentalis* Kanouse, Mycologia 28: 47. 1936.

Sporocarps subglobose to elongate or much lobed, 1-6(-10) mm broad, smaller specimens usually indented at base, the larger often with a basal opening that extends into a central cavity; bright orange-yellow when moist, becoming light yellow to nearly white when dry. Peridium thin, white, composed of loosely interwoven, thick-walled hyphae 1-8  $\mu$  diam. Gleba containing coarse, vesicular, thin-walled hyphae up to 15  $\mu$  diam, often becoming crushed between the crowded zygospores. Zygospores globose, ellipsoid or obovoid,  $27-75(-83) \times 27-65(-75) \mu$ ; walls hyaline to pale yellow, up to 10  $\mu$  thick, composed of an outer wall up to 3  $\mu$  and a thicker, inner wall up to 8  $\mu$ ; spore contents of deep-yellow oil globules that often fade to light yellow. Gametangia parallel, equal or subequal in size, thin-walled and ephemeral, observed only on immature spores, uniting at or near their tips, the zygospores budding mostly from the point of union but occasionally forming above one gametangium.

DISTRIBUTION, HABITAT, AND SEASON: Hypogeous or epigeous, widely distributed in mountains up to timberline and occasionally at low elevations. In soil or humus, on coniferous litter, wood or bark of fallen trees (conifers, *Alnus*), or old fruiting bodies of Polyporaceae (e.g. *Ganoderma*, *Fomes*, or *Polyporus*). Fruiting after heavy rains in late summer or autumn through winter, and in spring and early summer, when it is often found under the edges of melting snowbanks. To date no Northwestern collections have been made from sphagnum, a common habitat of the species in eastern North America and Europe.

MYCORRHIZAL ASSOCIATIONS: Apparently a saprophyte or mycoparasite. Mycorrhiza formation, if it occurs, must be a facultative habit.

ETYMOLOGY: Latin, *pisiformis* (pea-shaped).

COLLECTIONS EXAMINED: ALASKA—Ketchikan, leg. L. D. Parks

(UC 62495). BRITISH COLUMBIA—Vancouver, leg. R. Bandoni and P. Perrin (UBC 5335). Manning Park, leg. S. G. Brough, 11 May 1967 (UBC). CALIFORNIA—*Del Norte Co.*: Trappe 2781 (OSC). *Humboldt Co.*: H. E. Parks 6550 (UC 139202). *Siskiyou Co.*: leg. W. J. Sundberg, Trappe 3237 (OSC). OREGON—*Benton Co.*: Trappe 1901 (OSC). *Clackamas Co.*: Trappe 2160, 2161 (OSC). *Coos Co.*: Trappe 2707 (OSC). *Curry Co.*: Trappe 2783 (OSC). *Douglas Co.*: Trappe 2785 (OSC). *Hood River Co.*: A. Rossman 586 (OSC). *Jefferson Co.*: Trappe 1823 (OSC). *Josephine Co.*: Takilma, 29 November 1925, leg. C. A. Brown (MICH, paratype of *E. occidentalis* Kanouse). *Klamath Co.*: Crater Lake Nat. Park, Trappe 2193 (OSC). *Lane Co.*: Trappe 2716, 2846, 3202 (OSC). *Lincoln Co.*: Trappe 2278 (OSC). *Linn Co.*: Trappe 719, 2801, 2802 (OSC). *Marion Co.*: Trappe 773 (OSC). *Polk Co.*: Trappe 2447, 2819 (OSC). *Tillamook Co.*: Trappe 2383, 2659 (OSC). *Wasco Co.*: Trappe 1826 (OSC). *Yamhill Co.*: Trappe 2816 (OSC). WASHINGTON—*Grays Harbor Co.*: Lake Quinalt, November 1925, C. A. Brown (MICH, paratype of *E. occidentalis*). *King Co.*: Hosford 802 (CWSC); leg. R. Fogel, Trappe 3137 (OSC). *Lewis Co.*: Trappe 1866 (OSC). *Mason Co.*: Trappe 1876 (OSC). *Pierce Co.*: Mt. Rainier Nat. Park, Smith 28825, 29371, 30894 (MICH). *Whatcom Co.*: North Cascades Nat. Park, Trappe 1822, 2011, 2012 (OSC).

In the Northwest this species is collected more frequently than any other *Endogone*. When wet, sporocarps are a bright, deep yellow and conspicuous in spite of their small size, but on drying they become pallid and more difficult to see. Since this is one of the few *Endogone* species that can be collected with some regularity, it should be useful for taxonomic and physiologic studies.

A number of collections of typical *E. pisiformis* from Europe and eastern North America have been examined and compared with collections from Oregon and Washington. Several collections from the Northwest have spores with larger maximum sizes than were observed in any eastern collections. The largest spores found in eastern sporocarps were 60  $\mu$  in length while spores in some northwestern collections range up to 83  $\mu$ . Also the spore walls in nearly all northwestern collections are thicker than those found in the eastern ones; the maximum wall thickness for eastern collections examined was 6  $\mu$ , while spore walls up to 10  $\mu$  thick were observed in some western collections. The extremes of the two groups would seem to represent two distinct taxa. However, the differentiating characters intergrade, and it would be difficult or impossible to distinguish certain western collections with unusually small spores and thin walls from eastern collections with unusually large spores and thick walls.

Kanouse (1936, p. 62) named the western form of this species *E. occidentalis* and stated that it differed "in habitat, in absence of sporangia



in culture, in smaller size and paler color of the sporocarps." In eastern North America, *E. pisiformis* is most often found near the tips of sphagnum, a habitat that has not been reported for it in the West, but it has also been collected in the East from various other substrates: "on leaves, twigs, dung, rotten logs, etc., in moist situations, especially coniferous woods" (Thaxter, 1922, p. 299). It is generally epigeous, but also fruits in the leaf litter or soil.

The two paratypes (MICH) cited in the original description of *E. occidentalis* were examined and found to differ from the typical *E. pisiformis* of eastern North America only in having slightly larger spores with thicker walls. In both collections the spores are mature and gametangia are not visible. The unusual "spore attachments" illustrated by Kanouse (1936, figs. 26-32) probably are not gametangia but merely glebal hyphae. The gametangia of *E. pisiformis*, especially in the western form, are very thin-walled and ephemeral and normally are not observable on mature spores.

5. *Endogone incrassata* Thaxter, Proc. Am. Acad. Arts Sci. 57: 305-306. 1922.

FIG. 5

Sporocarps 1.5-5 mm diam, globose to subglobose, ochraceous, surface wrinkled and appearing incrustated; larger sporocarps hollow, containing a single cavity lined with sterile hyphae; small sporocarps solid, lacking any trace of a cavity. Peridium 10-70  $\mu$  thick, composed of slender, thick-walled hyphae 1-4  $\mu$  diam. Gleba in hollow specimens 0.5-1 mm or slightly more in thickness. Zygospores embedded in a matrix of coarse, vesicular, thin-walled hyphae, not enclosed in a hyphal mantle, scattered thickly throughout the gleba without any definite arrangements, spherical, obovoid, or ellipsoid, 55-110  $\times$  45-75  $\mu$ . Spore walls 4-10  $\mu$  thick, consisting of an outer wall 2-7  $\mu$  with a small opening at the base and a continuous inner wall 2-3.5  $\mu$ ; outer wall thicker than the inner in most spores. Gametangia shrunken and not clearly discernible. Odor, when fresh, distinctly of onions.

DISTRIBUTION, HABITAT, AND SEASON: Known in the Northwest from only one collection in Alaska. Hypogeous to epigeous in moss and coniferous litter of a *Picea-Tsuga* forest, October. Also in Maine (Thaxter, 1922).

MYCORRHIZAL ASSOCIATIONS: Unknown.

ETYMOLOGY: Latin, *incrassatus* (thickened), apparently in reference to the swelling of spore walls when mounted in KOH.

COLLECTIONS EXAMINED: ALASKA—Kenai Peninsula, Wells-Kempton 3017 (OSC and Wells-Kempton Herbarium).

The sporocarps of this species are similar in size to those of *E. pisiformis*. The two species apparently differ from each other in a number of respects, but since *E. incrassata* is known from only three collections

(two by Thaxter from Maine), its variability is not well known. The following differences appear consistent:

<i>E. pisiformis</i>	<i>E. incrassata</i>
Sporocarps:	
Whitish when dry, subspherical to lobed and convolute, when hollow with opening to exterior.	Ochraceous when dry, subspherical to lobed, when hollow without opening to exterior.
Spores:	
Maximum length 83 $\mu$ , but only rarely over 75 $\mu$ .	Maximum length 110 $\mu$ , commonly over 90 $\mu$ .
Spore walls:	
Outer wall thin, inner wall thick.	Outer wall thick, inner wall thin.
Odor:	
None.	Of onions.

When mounted in water or lactophenol, the greatly thickened exospore walls described by Thaxter (1922) for "fully matured" spores were not observed. However, when sections were mounted in 5% KOH the outer walls of cut spores quickly become greatly swollen and crush the inner walls. Such spores resemble Thaxter's Fig. 19, later reproduced by Zycha (1935) and Zycha et al. (1969). For further information on this species see Gerdemann and Trappe (1970).

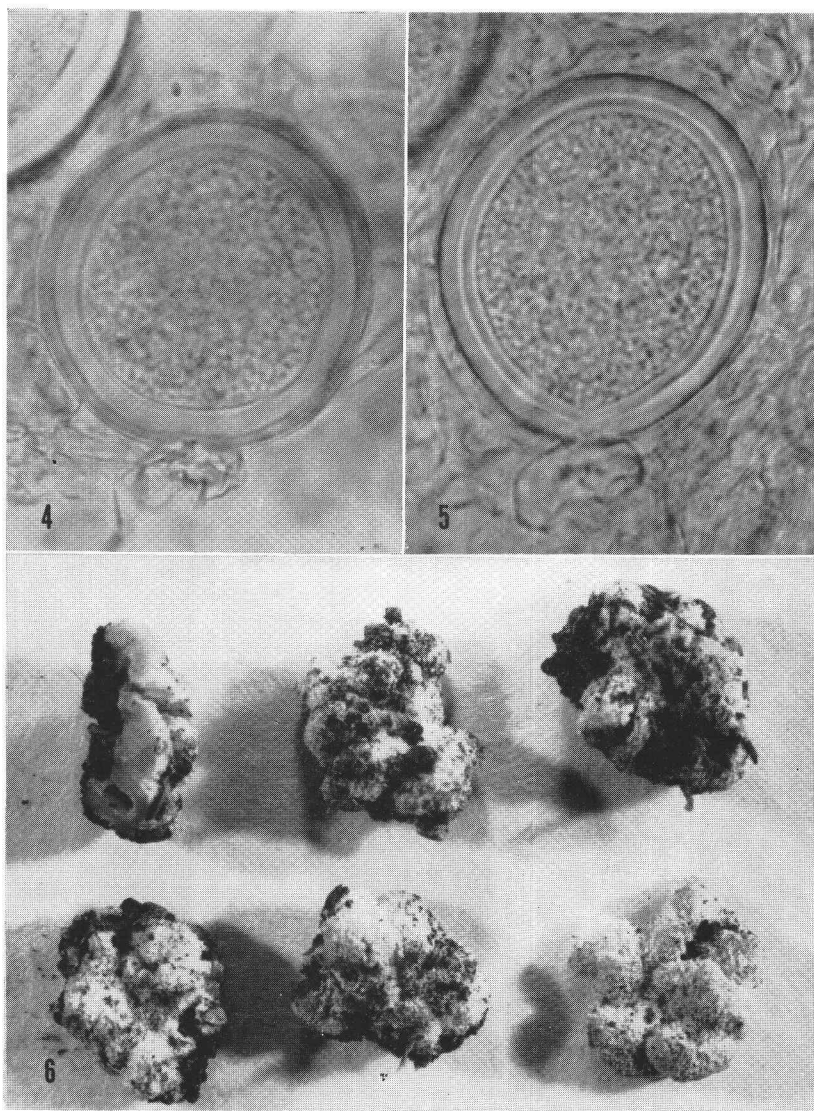
**6. *Endogone verrucosa* Gerdemann & Trappe, sp. nov.**

Sporocarpia 10 mm lata, irregulariter globosa, pallide crocea, minute verrucosa, sine peridio. Gleba e zygosporarum globulis globosis vel subglobosis 340-600  $\mu$  latis in palla hypharum arcte intextarum, tenuium, crasse tunicatarum inclusis composita, globulis stipatis vel spatio separatis. Zygosporae globosae, ellipsoideae, vel ovoideae, 28-57  $\times$  25-45  $\mu$ , tunicis 2-5  $\mu$  crassis, exteriore 1  $\mu$  vel minus crassitudine. Sporae stipatae vel ab hyphis crasse tunicatis hyalinis separatae, haud in hypharum palla inclusae. Odos suavis, saccharum ambustum vel Cocoli nuciferae carnem in memoriam reducens.

Sporocarp 10 mm broad, irregularly globose, pale yellow, minutely verrucose; peridium absent. Gleba of globose to subglobose zygospore clusters 340-600  $\mu$  broad, each cluster enclosed in a layer of tightly woven, slender, thick-walled hyphae; spore clusters compacted together or separated by open space. Zygospores globose to ellipsoid or obovoid, 28-57  $\times$  25-45  $\mu$ ; spore walls 2-5  $\mu$  thick, the outer wall 1  $\mu$  or less thick. Spores compacted together or separated by thick-walled hyaline hyphae. Individual spores not enclosed in a hyphal mantle. Gametangia not observed. Odor when fresh fragrant, like burnt sugar or coconut.

DISTRIBUTION, HABITAT, AND SEASON: Known only from the type collection.

MYCORRHIZAL ASSOCIATIONS: Unknown.



FIGS. 4-5. Zygospores of *Endogone*,  $\times 625$ . 4. *Endogone pisiformis*, showing the thin outer-wall and thick inner-wall. 5. *Endogone incrassata*, showing the thick outer-wall and thin inner-wall. Fig. 6. Sporocarps of *Endogone acrogena*, cross-sectional view of specimen in upper left hand corner, upper surface of other specimens,  $\times 6.4$ .

ETYMOLOGY: Latin, *verrucosus* (warty), referring to the surface configuration of the sporocarp.

COLLECTION EXAMINED: TYPE: ALASKA—Kenai Peninsula, Turnagain Pass, hypogeous in needle duff, *Picea-Tsuga* forest, 26 September 1963, Wells-Kempton 3019 (OSC).

Although gametangia were not observed, the absence of hyphal attachments to the spores, the continuous inner spore wall, and spore contents of nearly uniform size clearly indicate the zygosporic nature of the species.

This species is most nearly related to *E. oregonensis*. *Endogone verrucosa* differs in that the sporocarp lacks a peridium, the spores are much smaller and have a very thin outer spore wall, and the hyphae in the gleba are thick-walled. Also, the spore clusters of *E. verrucosa* are enclosed in an endoperidium of interwoven thick-walled hyphae, whereas the spore clusters in *E. oregonensis* lack a distinct endoperidium and are separated from each other by bands of thin-walled hyphae and soil.

### 7. *Endogone oregonensis* Gerdemann & Trappe, sp. nov. FIGS. 7, 8

Sporocarpia globosa vel ellipsoidea vel lobata et irregularia, 6–20 mm diametro, in peridio tenui, albo, byssoideo cui solum multum adhaerat inclusa. Gleba secta laticem album exsudens, globula pallida vel pallide sordide lutea sporarum ad 2 mm diametro continens a laminis soli vel hypharum albarum separata. Zygosporae pallide croceae, globosae, ellipsoideae, vel ovoideae, 77–150 × 44–120  $\mu$ , tunica 5–7  $\mu$  crassa e laminis duobus composita, exteriore hyalina vel pallide crocea et plerumque paulo quam interior hyalina crassiore, haud in hypharum palla inclusae, ab hyphis tenuiter tunicatis vesicularibus frequenter inter sporas coartas compressis separatae. Gametangia ephemera, nisi in sporis immaturis invisae, aequa vel subaequa, ad vel prope apices coeuntia, zygosporam ad vel prope juncturam vel ex gametangio altero producentia.

Sporocarps globose to ellipsoid or lobed and irregular, 6–20 mm broad, enclosed in a thin, white, cottony peridium with much adhering soil. Gleba exuding white latex when cut, containing pallid to pale sordid yellow, globose clusters of spores up to 2 mm broad, spore clusters separated from each other by bands of soil or white hyphae. Zygosporae pale yellow, globose to ellipsoid or ovoid, 77–150 × 44–120  $\mu$ ; spore wall 5–7  $\mu$  thick, composed of two layers, the outer wall hyaline to pale yellow and generally slightly thicker than the hyaline inner wall; spores not enclosed in a hyphal mantle, separated from each other by thin-walled vesicular hyphae which are often crushed between the thickly crowded spores. Gametangia ephemeral, observed only on immature spores, equal or subequal in size, uniting at or near their tips with the zygosporae budding from near the point of union or from one of the two gametangia.

DISTRIBUTION, HABITAT, AND SEASON: Hypogeous, known only from the northwest Oregon coast and Coast Range in coniferous forests (*Picea*, *Pseudotsuga*, *Tsuga*) at elevations less than 500 m. Collected in June, July, September, and November.

MYCORRHIZAL ASSOCIATIONS: Unknown, but probably ectomycorrhizal with *Pseudotsuga menziesii*.

ETYMOLOGY: *Oregonensis* (growing in Oregon).

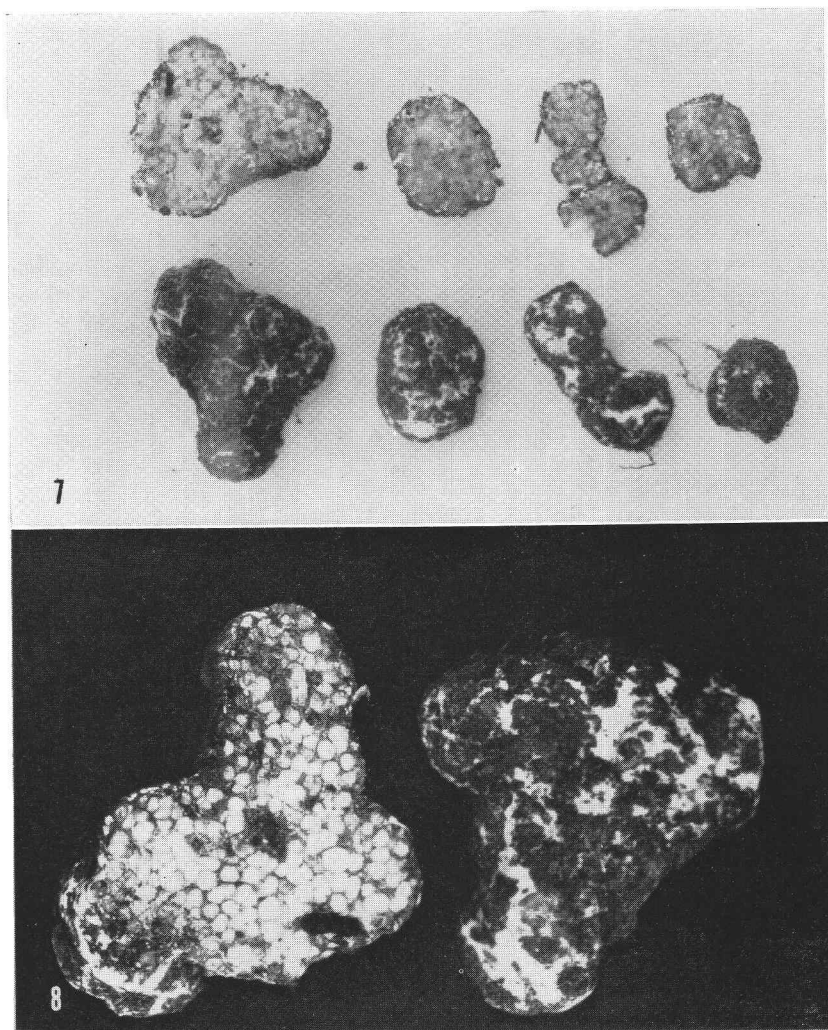
COLLECTIONS EXAMINED: TYPE: OREGON—*Lincoln Co.*: Green Point, Cascade Head, elev. ca. 250 m, hypogeous under old growth *Pseudotsuga menziesii* and *Tsuga heterophylla*, 19 July 1966, Trappe 741 (OSC). PARATYPES: OREGON—*Lincoln Co.*: Trappe 1975 (OSC). *Polk Co.*: Trappe 2452 (OSC). *Tillamook Co.*: Trappe 872 (OSC).

This species resembles *E. multiplex* Thaxter in having zygospores formed in globose clusters. However, it differs significantly in a number of points. The sporocarps of *E. oregonensis* are enclosed in a peridium; a peridium is not present on the type specimen of *E. multiplex*. The individual zygospores of *E. multiplex* are enclosed in a "clearly defined, relatively thick, separable envelope, 8–12  $\mu$  thick, of close felted hyphae" (Thaxter, 1922, p. 302), while spores of *E. oregonensis* are not enclosed in an envelope. Hyphae in the sporocarp of *E. multiplex* are thick-walled and brittle, whereas the hyphae in sporocarps of *E. oregonensis* are vesicular, very thin-walled, and often crushed between the spores. Although the type specimen of *E. multiplex*, examined by the senior author, is mature and gametangia are not visible, it is apparent from the indentations on spore walls that the two gametangia were attached to many of the spores at some distance from each other. Gametangia of *E. oregonensis* are attached to spores at only one point.

#### 8. *Endogone acrogena* Gerdemann, Trappe & Hosford, sp. nov. FIG. 6

Sporocarpia ad  $4 \times 7 \times 10$  mm, valde lobata, convoluta irregulariaque e textu complicato ad 2 mm crasso constructa, viva spendide crocea, sicca pallide lutea. Peridium verum nullum. In sporocarpis crescentibus hyphae glebae e superficie radiantes, in maturis ad superficiem implicatae, emissae. Gleba acrogene e basi sterili vel substerili ex hyphis intertextis composito ut hyphae radiantes cum zygosporarum seriebus frequenter arcte in catenulis appressarum intermixtae evolvens; spora maturissimae basales, novissimae ad superficiem crescentem evolventes. Zygosporae magnitudine et forma variae,  $15 \times 30\text{--}80 \times 59$   $\mu$ , e catenula matura parvae vel magnae, globosae, ellipsoidales, ovatae, vel irregulares, a compressione applanatae et angulares. Sporarum tunica ad 5  $\mu$  crassa, e lamellis duobus variabilibus composita. Gametangia  $15 \times 7$   $\mu$ , tenuiter tunicata, ephemera, aequa, parallela, ad apices coeuntia, zygosporam super juncturam producentia.

Sporocarps up to  $4 \times 7 \times 10$  mm, greatly lobed, convoluted and irregular, formed from folded tissue up to 2 mm in thickness, bright yellow when fresh, light tan-yellow when dry. True peridium absent. In developing sporocarps, tufts of glebal hyphae radiate from the surface, becoming matted over the surface by maturity. Gleba developing acrogenously from a sterile or nearly sterile base of interwoven hyphae as radiate hyphae intermingled with radiate rows of zygospores that are often tightly adpressed in chains, the oldest spores at the base, the youngest at the actively growing surface. Zygospores variable in size and



FIGS. 7-8. Sporocarps of *Endogone oregonensis*, surface and cross-sectional views, showing the white peridium with much adhering soil and gleba with globose clusters of zygospores separated from each other by bands of hyphae and soil. 7.  $\times 1.4$ . 8.  $\times 3.75$ .

shape,  $15 \times 30-80 \times 59 \mu$ , mature spores within a chain varying from small to large, globose, ellipsoid, ovate or irregular, becoming flattened and angular from pressure. Spore wall up to  $5 \mu$  thick, of two variable layers. Gametangia  $15 \times 7 \mu$ , thin-walled and ephemeral, equal in size, parallel, uniting at their tips, with the zygospore forming above the point of union.

DISTRIBUTION, HABITAT, AND SEASON: Epigeous, known only from the Cascade and Olympic Mountains of Washington from low elevations to near timberline. Fruiting on soil surface or on mosses. May, September, and October.

MYCORRHIZAL ASSOCIATIONS: Unknown.

ETYMOLOGY: Latin, *acrogenus* (born at apices), referring to the acrogenous development of spores in rows.

COLLECTIONS EXAMINED: TYPE: WASHINGTON—*Snohomish Co.*: End of White Chuck River Road, 17 October 1967, Hosford 232 (OSC). PARATYPES: WASHINGTON—*Jefferson Co.*: Olympic Nat. Park, Smith 13071 (MICH). *Pierce Co.*: Mt. Rainier Nat. Park, Hosford 65 (OSC).

This is a most interesting species. Although acrogenous development of sporocarps is known in chlamydosporic species, it has not previously been reported for zygosporic types. The gametangia are ephemeral and difficult to observe, being visible only on very young spores at the actively growing surface of a sporocarp. Since gametangia are not visible on mature spores, the appearance of the spores tightly compacted in chains deceptively suggests that they form by acrogenous budding.

#### EXTRALIMITAL SPECIES

9. *Endogone multiplex* Thaxter, Proc. Am. Acad. Arts Sci. 57: 301–302. 1922.

See Thaxter (1922) for a description of this species, which is known only from the type collection from under leaf litter in a *Quercus-Carya* woods on Cutts Island, Maine (Thaxter 5202, FH). Its relationship to *E. oregonensis* and *E. stratosa* is discussed under our descriptions of those species.

10. *Endogone tuberculosa* Lloyd, Lloyd Mycol. Writings 5 (Mycol. Notes 56): 799. 1918.

Thaxter (1922, p. 304) described this species as having spores "surrounded by a thin, but as a rule clearly defined, envelope of closely matted finer hyphae." Our examination of the type (Lloyd 7237, BPI; isotype, Thaxter 5179, FH), revealed that the "envelope" is simply glebal hyphae compacted by spore enlargement. The tissue is not adherent to the spore surface, as is the case with *E. multiplex* and *E. stratosa*. The greatly thickened exospore walls reported by Thaxter for *E. tuberculosa* were likely produced by mounting in KOH. *Endogone tuberculosa* is known only from the type collection from New South Wales, Australia. It differs from all other *Endogone* species in that the relatively large sporocarp consists of greatly convoluted strata which enclose considerable soil.

11. *Endogone alba* (Petch) Gerdemann & Trappe, comb. nov.

≡ *Sclerocystis alba* Petch, Ceylon J. Sci. Sec. A. Ann. Roy. Bot. Gard. Peradenya. 9: 322-323. 1925.

This species resembles *Sclerocystis coremioides* Berk. & Broome in having small ovoid sporocarps aggregated and fused together in masses. However, the spores appear to be zygosporae rather than chlamydospores, and they are distributed at random within the gleba. No traces of gametangia are evident on the spores; however, the absence of hyphal attachments and the spore contents consisting of oil globules of nearly uniform size are good evidence for their zygosporic nature. This species is unusual in several respects. It produces the smallest sporocarps of any *Endogone*, and it is the only species with sporocarps fused in masses. As far as we are aware it is the only species that has been found in a tropical region. However, the type locality is given as Hakgala, which very likely refers to the Hakgala Botanical Garden on Mount Hakgala at 5,600 ft. elevation. It has a cool temperate climate with a mean annual temperature of 61° F. It is also of interest that *Fagus*, *Quercus*, and *Betula* species were grown in the garden.

II. GIGASPORA Gerdemann & Trappe, gen. nov.

Type species: *Gigaspora gigantea* (Nicolson & Gerdemann)  
Gerdemann & Trappe

Azygosporae in solo singillatim productae, magnae, plerumque globosae vel subglobosae, plasma oleosum includentes, in cellula bulbosa instar suspensoris plerumque ab hypha angusta cum spora conjuncto terminaliter efformatae. Sporae tunica continua, poro parvo ocluso excepto. Tubuli germinativi tunicam prope basim sporae directe penetrantes. Vesiculi tenuiter tunicati in solo a hyphis contortis singillatim vel gregatim efformati. Endomycorrhizae arbusculis insignis particeps.

Azygosporae produced singly in soil, large, generally globose or subglobose, with oily contents, borne terminally on a bulbous suspensor-like cell, usually with a narrow hypha extending from the suspensor-like cell to the spore. Spore wall continuous except for a small occluded pore. Germ tubes produced directly through wall near spore base. Thin-walled vesicles borne in soil on coiled hyphae, forming singly or in clusters. Forming endomycorrhizae with arbuscles.

ETYMOLOGY: Greek, *giga-* (giant) and *-spora* (spore), referring to the exceptionally large spores typically produced by members of the genus.

The spores formed by members of this genus have been previously called zygosporae (Nicolson and Gerdemann, 1968). They resemble zygosporae in many respects; however, they do not appear to form from the union of two gametangia. In order to distinguish them from the true zygosporae of *Endogone* species we have chosen to refer to them as azy-



gospores. A detailed study of their developmental morphology is needed to determine their exact nature. The spore walls of *Gigaspora* species are continuous except for a very small, occluded pore. The spore is borne on a bulbous, suspensor-like structure which generally has a slender hypha extending from it to the spore. There is, however, no obvious sexual fusion. In contrast to chlamydospores which "germinate" by re-growth of subtending hyphae, the spores of *Gigaspora* species produce germ tubes directly through the spore wall in the base region.

Each species of *Gigaspora* produces distinctive vesicles on coiled hyphae in the soil. These structures fill with oil globules, and their function appears to be temporary storage of food. Perhaps such vesicles represent vestigial sporangia with a modified function. Another possibility is that they may be modified subsporangial vesicles. Since these vesicles remain thin-walled and are not cut off from subtending hyphae by septa, they would not appear to be comparable to the gemmae formed by the Mortierellaceae, as suggested by Zycha et al. (1969).

Sporocarps have not been observed, and the azygospores are produced singly in the soil. A determination of the relationships of this genus to *Endogone* is probably dependent upon the successful germination of zygospores of the latter.

*Gigaspora* species possess a type of hyphal wound healing that has not been reported for any other fungi (Gerdemann, 1955b).

Our spore descriptions are from structures readily observable in whole or crushed mounts examined under a light microscope. The spore wall in particular is probably much more complex than is indicated in most of our descriptions. In *G. gilmorei* Trappe & Gerd. the spore wall is transparent and the wall layers are thicker than in most other species. In *G. gilmorei* it is apparent that the spore wall structure and method of germination is very similar to that described by Mosse (1970a, b, c) for "honey-coloured sessile *Endogone* spores" (*Acaulospora laevis* Gerd. & Trappe). Therefore it is likely that the genera *Gigaspora* and *Acaulospora* are closely related.

*Gigaspora* species produce endomycorrhizae with arbuscules. Vesicles within roots have not been observed. Spores can be collected by wet-sieving and decanting and pot culture methods. They have been found in cultivated soils, native grasslands and in forests containing endomycorrhizal hosts.

#### KEY TO THE SPECIES OF GIGASPORA

- |   |                        |
|---|------------------------|
| 1. Azygospores hyaline to yellow or yellowish green, smooth .....   | 2                      |
| 1. Azygospores light to dark brown .....  | 4                      |
| 2. Spores hyaline when fresh, with brown suspensor-like cells and brown, knobby, clustered soil-borne vesicles .....                    | 12. <i>G. gilmorei</i> |
| 2. Spores hyaline to yellow or greenish-yellow with concolorous suspensor-like cells and smooth to echinulate soil-borne vesicles ..... | 3                      |

3. Globose spores less than 300  $\mu$  diam; vesicles smooth to knobby, formed singly ..... 13. *G. calospora*
3. Globose spores generally larger than 300  $\mu$ ; vesicles echinulate, formed in clusters ..... 14. *G. gigantea*
4. Globose spores larger than 300  $\mu$ , ornamented with scattered, irregularly shaped, hyaline warts and ridges  $\pm 2 \mu$  tall; vesicles coralloid ..... 15. *G. coralloidea*
4. Globose spores less than 300  $\mu$ , ornamented with minute spines; vesicles smooth (extra-limital species) ..... 16. *G. heterogama*

## 12. *Gigaspora gilmorei* Trappe & Gerdemann, sp. nov.

*Azygosporeae* in solo singillatim efformatae, 204–320  $\mu$  diametro, globosae, subglobosae, vel quandoque ellipsoideae quam longitudo latiores, hyalinae. Sporarum tunica facile in tunicas duas separans, externam hyalinam, fragilem, ad 11  $\mu$  crassam, e lamella exteriore tenui ad 1  $\mu$  crassa et interiori crassa consistentem, internam hyalinam, flexibilem, ad 7.4  $\mu$  crassam, e lamella exteriore minus quam 1  $\mu$  crassitudine en interioribus tribus crassitudine variabilibus consistentem. Maturitate, plerumque prope spora basim, lamellae duae intimae tunicae internae a tertia secedentes in sporam intrusae, spatium periphericum seponentes; postea tunicae materia additica super lamellas sejunctas deposita, lamellaeque radiantes spatia majora in minora separantes constructae. Tubae germinativae e spatiis minoribus ortae per tunicam externam extrusae. Cellula instar suspensoris 27–40  $\mu$  lata, pallide brunnea, claviformis, tunicis aliquantum incrassatis, 1–1.5  $\mu$  prope sporam, induta, vulgo sub apice inflato septata. Hyphae e cellula suspensoriformi per brevem spatium incrassata pallide brunnea, ad instar clavi lignei efformata, secundum spora superficiem hyalina, tenuiter tunicata, septata, senescens ad clavum tantum redacta. Vesiculae in solo ortae, e hyphis stricte glomeratis natae, circulos 3–14 numero 15–25  $\mu$  diametro constantes, tenuiter tunicatae, hyalinae in colore pallide brunneum evadentes, irregulares, umbonibus confertis ornatae, 3–6  $\times$  4–9  $\mu$ . Endomycorrhizae arbusculis praeditae particeps.

*Azygospores* formed singly in soil, 204–320  $\mu$  diam, globose to subglobose or occasionally ellipsoid and then broader than long, hyaline. Spore wall readily separating into an inner and outer wall. Outer wall hyaline, brittle, up to 11  $\mu$  thick, consisting of a thin outer layer up to 1  $\mu$  and a thick inner layer. Inner wall hyaline, flexible, up to 7.4  $\mu$  thick, consisting of a thin outer membrane less than 1  $\mu$  and three inner layers of variable thickness. At maturity, generally near the spore base, the two innermost layers of the inner wall separate from the third layer and bulge into the spore to produce a peripheral compartment. New wall material is deposited upon the separated membranes and radial walls form to divide large compartments into smaller ones. Germ tubes from the small compartments penetrate the outer wall. Suspensor-like cell 27–40  $\mu$  broad, light brown, clavate, the walls slightly thickened, 1–1.5  $\mu$  near the spore, generally septate below the swollen apex. Hypha from the suspensor-like cell thickened and light brown for a short distance and appearing as a peg, becoming hyaline, thin-walled and septate along the spore surface, with age only the peg persisting. Vesicles in soil, borne on tightly coiled hyphae in clusters of 3–14, 15–25  $\mu$  diam, thin-walled, hyaline changing to pale brown, irregular with crowded knobs 3–6  $\times$  4–9  $\mu$ . Forming endomycorrhizae with arbuscules.

DISTRIBUTION, HABITAT, AND SEASON: Known from dune and beach sands in western Oregon and an apple orchard near the central coast of California. Field collections in Oregon have been made in December and February. Probably present in soil throughout the year. Spores develop abundantly in sand pot cultures within 6 months after inoculation.

MYCORRHIZAL ASSOCIATIONS: Associated with endomycorrhizae of *Hypochaeris radicata* L. and *Malus* sp. in the field and forming endomycorrhizae with *Fragaria* sp. and *Allium cepa* L. in pot culture.

ETYMOLOGY: (Gilmore's), in honor of A. E. Gilmore, the discoverer of the species.

COLLECTIONS EXAMINED: TYPE: CALIFORNIA—*Santa Cruz Co.*, Freedom, inoculum from an apple orchard mixed with autoclaved sand and planted with *Fragaria* runners; spores retrieved 22 May 1970, A. E. Gilmore pot 107, Trappe 2175 (OSC). PARATYPES: CALIFORNIA—*Santa Cruz Co.*, Trappe 2530 (OSC). OREGON—*Coos Co.*: leg. Iwan Ho, Trappe 2594 (OSC). *Lincoln Co.*: leg. Iwan Ho, Trappe 2561 (OSC).

*Gigaspora gilmorei* is readily distinguished from other members of the genus in having colorless spores with brown suspensor-like cells, knobby, brown vesicles, and brown germ tubes. The spore walls become brown with storage in lactophenol. The wall structure, which in this species is readily visible in whole mounts, and the method of germination, are very similar to those described by Mosse (1970a, b, c) for "honey-coloured sessile *Endogone* spores" (*Acaulospora laevis*).

When spores are placed in zinc-chlor-iodide the innermost membrane stains blue indicating the presence of cellulose or hemicellulose. All other wall layers and hyphae stain yellow.

13. *Gigaspora calospora* (Nicol. & Gerd.) Gerdemann & Trappe, comb. nov.

≡ *Endogone calospora* Nicol. & Gerd., *Mycologia* 60: 322. 1968.

Azygospores formed singly in soil, 150–285 × 165–412 μ, globose to ellipsoid or oblong, the globose specimens less than 300 μ diam, pale yellow to greenish yellow. Spore walls 3–5 μ thick, continuous except for an occluded pore at the attachment, enclosing a thin inner membrane. Suspensor-like cells 33–48 μ diam, bulbous, the walls concolorous with spore walls and thin or up to 3(–5) μ thick, usually giving rise to a slender hypha that projects to the spore. Vesicles 23–33 μ diam, subglobose, hyaline to pale brownish yellow, thin-walled, smooth, subglobose to somewhat irregular or knobby, borne singly on coiled hyphae in the soil.

DISTRIBUTION, HABITAT, AND SEASON: Relatively common along the Oregon and Washington coasts in sand dunes and soil and in the Willa-

nette Valley of Oregon; also east of the Cascade Range in Oregon and Washington in orchards, open pine forests, and semi-desert mountains at elevations up to 2800 m. Wet-sieved from soils collected throughout the year. Spores develop abundantly in pot culture in 3½–6 months. Illinois and Scotland (Nicolson and Gerdemann, 1968), England and New Zealand (as "bulbous reticulate spores:" Mosse and Bowen, 1968a, b).

MYCORRHIZAL ASSOCIATIONS: Associated with endomycorrhizae of *Abronia latifolia* Eschsch., *Artemisia* sp., *Chamaecyparis lawsoniana* (A. Murr.) Parl., *Festuca* spp., *Fragaria chiloensis* (L.) Duch., *Hypochaeris radicata*, *Lolium* sp., *Lupinus* sp., *Malus* spp., *Prunus* sp., *Thuja plicata* Donn, and *Triticum aestivum* L. in the field and forming arbuscular, vesicle-lacking endomycorrhizae with *Allium cepa*, *Fragaria vesca* L., *Lycopersicon esculentum* Mill., and *Zea mays* in pot culture.

ETYMOLOGY: Greek, *calo-* (beautiful) and *-spora* (spore).

COLLECTIONS EXAMINED: OREGON—*Benton Co.*: leg. Iwan Ho, Trappe 2159, 2206, 2211, 2212 (OSC). *Coos Co.*: leg. Iwan Ho, Trappe 2612, 2742 (OSC). *Curry Co.*: leg. Iwan Ho, Trappe 2739 (OSC). *Deschutes Co.*: leg. Iwan Ho, Trappe 2732, 3522 (OSC). *Grant Co.*: leg. Iwan Ho, Trappe 3261 (OSC). *Harney Co.*: leg. Iwan Ho, Trappe 3508, 3511 (OSC). *Lane Co.*: leg. Iwan Ho, Trappe 2741, 2845 (OSC). *Lincoln Co.*: Trappe 2102, 2754 (OSC): leg. Iwan Ho, Trappe 2555, 2740 (OSC). *Linn Co.*: leg. Iwan Ho, Trappe 2163, 2203, 2570 (OSC). *Tillamook Co.*: leg. Iwan Ho, Trappe 2735, 3061 (OSC). WASHINGTON—*Chelan Co.*: leg. Edward Stahly, Trappe 2216, 2228, 3073 (OSC). *Clallam Co.*: leg. Iwan Ho, Trappe 3147 (OSC). *Grays Harbor Co.*: leg. Iwan Ho, Trappe 3143 (OSC). *Pacific Co.*: leg. Iwan Ho, Trappe 3144, 3155 (OSC).

The color of the northwestern specimens tends to be brighter, the spore walls thicker, and the vesicles more knobby than originally described for this species. However, these differences seem to reflect degrees of maturation, since relatively young collections in several northwestern collections match the type description exactly.

14. *Gigaspora gigantea* (Nicol. & Gerd.) Gerdemann & Trappe, comb. nov.

≡ *Endogone gigantea* Nicol. & Gerd., Mycologia 60: 321. 1968.

Azygospores formed singly in soil, 353–368 × 345–398 μ, globose to ellipsoid, greenish yellow, with a thin, outer wall tightly covering an inner wall, the inner wall 5–7 μ thick and continuous except for an occluded pore at the attachment. Suspensor-like cells bulbous, 42–48 μ diam, giving rise to a slender hypha that projects to the spore. Vesicles not observed, in this collection. For a more complete description see Nicolson and Gerdemann (1968).

DISTRIBUTION, HABITAT, AND SEASON: Known only from a single small collection wet-sieved from one pot of nonsterile greenhouse soil in which *Zea mays* had been grown for 4 months. The soil consisted of 3 parts sandy riverbottom soil from near Corvallis, Oregon, and 1 part Canadian peat. Common in midwestern U.S. (Gerdemann, 1955a; Nicolson and Gerdemann, 1968) and Florida (Schenck and Hinson, 1971).

MYCORRHIZAL ASSOCIATIONS: Known to form arbuscular, vesicle-lacking endomycorrhizae with *Zea mays*, and other cultivated crop plants (Gerdemann, 1955a), as well as *Liriodendron tulipifera* L., *Fraxinus americana* L., *Acer negundo* L., and *A. saccharum* Marsh. (Clark, 1969).

ETYMOLOGY: Latin, *giganteus* (giant), referring to the exceptionally large spores that the species often forms (up to 812  $\mu$  broad).

COLLECTIONS EXAMINED: OREGON—*Benton Co.*: Trappe 2103 (OSC).

The absence of this species from field collections to date in the Pacific Northwest leads to the suspicion that it may be strictly a "greenhouse species," possibly imported with the Canadian peat.

Mosse and Bowen (1968a) report "bulbous vacuolate spores" from Australia and New Zealand and equate these with Gerdemann's (1955a) "Type B" *Endogone* spores which Nicolson and Gerdemann (1968) subsequently described as *Endogone gigantea*. However, the New Zealand and Australian spores of Mosse and Bowen are much too small to be *Gigaspora gigantea*.

Endomycorrhizae formed by this species increased growth of several hardwood tree seedlings (Clark, 1969).

### 15. *Gigaspora coralloidea* Trappe, Gerdemann & Ho, sp. nov.

Azygospores in solo singillatim ortae, 308–393  $\times$  324–454  $\mu$ , globosae, subglobosae, vel ellipsoideae quam longitudo plerumque latiores, atro-brunneae, globulos oleosos aequos continentes. Spores tunica fusco-brunnea, 8–15  $\mu$  crassa, continua poro ocluso prope locum colligationis excepto, superficie verruculis intervallo lato inter se separatis forma irregularibus atque lineis elevatis 2  $\mu$  altis. 0.5–6  $\mu$  latis, frequenter e spora basi radiantibus ornata, lamellam hyalinam 1–2  $\mu$  crassam includens. Cellula suspensoriformis 55–64  $\mu$  lata, bulbosa, tunica pallide brunnea, ad 3  $\mu$  crassa induta, nonnumquam sub apice inflato septata, interdum lateraliter affixa, frequenter hypham inconspicuam instar clavi lignei angustam, luteam vel pallide brunneam, ad tunicam spora extensam. Hyphae pallide brunneae, crasse tunicatae saepe aggregatae et ad spora tunicam circum punctum colligationis appressae. Vesiculae in solo natae 25–30  $\times$  30–40  $\mu$  singillatim e hyphis tenuiter tunicatis glomeratis ortae, pallide luteo-brunneae, juvenes umbonibus ornatae, mox coralloideae, prominentiis stipatis, irregularibus, saepe furcatis 5–15  $\times$  4–7  $\mu$ , tunica fere 1  $\mu$  crassa, cum prominentiis paucis ad 10  $\mu$  inflatis interspersis praeditae.

Azygospores formed singly in soil, 308–393  $\times$  324–454  $\mu$ , globose to subglobose or ellipsoid and then usually broader than long, very dark brown, the contents evenly sized oil globules. Spore wall dark brown, 8–15  $\mu$  thick, continuous except for occluded pore at attachment; surface ornamented with openly spaced and irregularly shaped hyaline warts

and ridges  $2\ \mu$  tall and  $0.5\text{--}6\ \mu$  broad, often tending to radiate out from the spore base; wall enclosing a hyaline membrane  $1\text{--}2\ \mu$  thick. Suspensor-like cell  $55\text{--}64\ \mu$  broad, bulbous, the walls light brown and up to  $3\ \mu$  thick, septate or not below the swollen apex, sometimes laterally attached, often producing an inconspicuous peg-like, narrow, yellow to pale brown hypha that extends to the spore wall. Light brown, thick-walled hyphae often clustered and appressed to the spore wall around the spore attachment. Soil-borne vesicles  $25\text{--}30 \times 30\text{--}40\ \mu$ , borne singly on thin-walled, coiled hyphae, light brownish yellow, knobby in youth, soon becoming coralloid with crowded, irregular, often forked projections  $5\text{--}15 \times 4\text{--}7\ \mu$  having walls  $\pm 1\ \mu$  thick intermingled with occasional thin-walled, inflated projections up to  $10\ \mu$  broad.

**DISTRIBUTION, HABITAT, AND SEASON:** Known only from dune sands on the Oregon coast. Collected in the field October to December. Probably present in soil throughout the year.

**MYCORRHIZAL ASSOCIATIONS:** Associated with *Fragaria chiloensis*, *Glehnia leiocarpa* Mathias, *Rumex acetosella* L., and grasses in the field and forming endomycorrhizae with *Glehnia* and *Allium cepa* in pot culture.

**ETYMOLOGY:** Latin, *coralloidea* (coral-form), referring to the form of the vesicles.

**COLLECTIONS EXAMINED: TYPE:** OREGON—*Tillamook Co.*: Sand Lake, in dunes, 27 October 1970, leg. Iwan Ho, Trappe 2538 (OSC). **PARATYPES:** OREGON—*Clatsop Co.*: leg. Iwan Ho, Trappe 3161 (OSC). *Tillamook Co.*: Trappe 2807 (OSC).

The dark spore color, warty surface, and coralloid vesicles readily distinguish *G. coralloidea* from other known species of *Gigaspora*.

#### EXTRALIMITAL SPECIES

16. *Gigaspora heterogama* (Nicol. & Gerd.) Gerdemann & Trappe, comb. nov.

≡ *Endogone heterogama* Nicol. & Gerd., Mycologia 60: 319–320. 1968.

Known only from the type collection (FH) from Illinois, this species differs from the other brown-spored member of the genus (*G. coralloidea*) in having spores covered with minute spines, suspensor-like cells often laterally attached to the spores, and smooth, clustered vesicles.

### III. ACAULOSPORA Gerdemann & Trappe, gen. nov.

*Type species: Acaulospora laevis* Gerd. & Trappe

Azygosporae in solo singillatim productae, magnae, plerumque globosae vel subglobosae, plasma oleosum includentes, in stipite vesiculi magni, terminalis, tenuiter tunicati lateraliter efformatae. Vesiculus magnitudine sporam subaequans,

maturus plasma ad sporam transfundens. Sporae tunica continua, poro parvo ocluso excepto. Tubuli germinativi tunicam prope basim sporae directe penetrantes. Endomycorrhizae vesiculis arbusculisque insignis particeps.

Zygosporae produced singly in soil, large, generally globose or subglobose, with oily contents, borne laterally on the stalk of a large, terminal, thin-walled vesicle. Vesicle about the same size as the spore, with vesicle contents transferred to spore at maturity. Spore walls continuous except for a small occluded pore. Germ tubes produced directly through walls near spore base. Forming endomycorrhizae with lobed vesicles and arbuscules.

ETYMOLOGY: Greek, *a-* (without), *caulos* (stem), and *spora* (spore), referring to the sessile spores.

The spores produced by *Acaulospora* spp. are best regarded as zygospores. They form in this way: A large vesicle with dense contents is produced terminally on a broad, funnel-shaped stalk. After the vesicle reaches its maximum size, the spore buds laterally from the stalk. The contents of the vesicle are then transferred to the spore and the emptied vesicle collapses (Figs. 9-14).

The nature of the vesicle in *Acaulospora* presents a difficult problem. It somewhat resembles the gametangia formed by *Syncephalis nodosa* van Tieghem, in which the zygospore buds laterally from a gametangium a considerable distance back from the point of conjugation (Thaxter, 1897). It also bears some resemblance to the larger of the two suspensors formed by *Mortierella elongata* Linnem. (Gams, Chien, and Domsch, 1972). The zygospore in this species forms laterally on a suspensor which has a diameter about the size of the spore. However, conjugation of gametangia has not been observed in *Acaulospora*, and the only apparent function of the vesicle is temporary storage of food. Its function, therefore, is probably very similar to that of the much smaller vesicles produced by *Gigaspora* species. It is unlikely, however, that the two types of structures are analogous.

Our descriptions are from structures readily observable in whole or crushed mounts examined with a light microscope. Mosse (1970a, b, c) examined sectioned spores of "honey-coloured, sessile *Endogone* spores," herein described as *Acaulospora laevis*, under light and electron microscopes. She determined that the spore wall in particular is much more complex than is indicated in our description. Mosse also described the formation of peripheral "compartments" within the spores from which the germ tubes are produced. These "compartments" are formed by separation of spore wall membranes. The two innermost membranes separate from the third and bulge into the spore. New wall material is deposited upon the split membranes and radial walls are formed which divide the large compartments into smaller ones. It is likely that this or a similar method of germination occurs throughout the genera *Acaulospora* and *Gigaspora*.

Spores occur singly in the soil and the species can be collected by wet-sieving and decanting or pot culture. Because of the unusual lobed vesicles it may be possible to recognize mycorrhizae formed by *Acaulospora laevis* in field collected material.

## KEY TO THE SPECIES OF ACAULOSPORA

1. Spores smooth ..... 17. *A. laevis*  
 1. Spores ornamented with minute, crowded spines, by maturity developing  
 an alveolate reticulum superimposed on the spines ..... 18. *A. elegans*

17. *Acaulospora laevis* Gerdemann & Trappe, sp. nov. FIGS. 9-14

Sporocarpia ignota. Sporae singulae in solo efformatae, sessiles, gestae a latere hyphae crassae tenuiter tunicatae in vesiculo globoso tenuiter tunicato prope terminatae. Vesicula sporae subaequa, ante sporae ortum adulta et materia densa, alba suffulta, sporis maturis exhausta et collapsa unde plerumque a collectione per cribri usum amissa. Sporae leves, 119-300 × 119-520 μ, globosae, subglobosae, ellipsoideae, vel nonnumquam reniformes vel irregulares. Sporae tunica paene continua, foramine ocluso excepto, e stratis tribus, exteriore rigido, luteo-brunneo vel rubro-brunneo, 2-4 μ crasso, medio hyalino, interiore hyalino, minute asperulo, composita, senescentia interdum minute perforata et delapsa. Sporae plasma in massulis globosis vel polyedri divisum, unde specie reticulatum. Sub loco colligationis sporae hyphas multas tenues ramosas 1-2.5 μ diametro proferens. Mycorrhizae vesiculis tenuiter tunicatis, lobatis atque arbusculis gaudentis particeps.

Sporocarps unknown. Spores forming singly in soil, sessile, borne laterally on a wide, thin-walled hypha 30-40 μ diam that terminates nearby in a globose, thin-walled vesicle. Vesicle approximately the same size as the spore, developing to full size prior to spore formation, with dense, white contents, becoming empty and shrunken at spore maturity and then usually lost in sieving. Spores smooth, 119-300 × 119-520 μ, globose to subglobose, ellipsoid or occasionally reniform to irregular, dull yellow in youth becoming deep yellow-brown to red-brown or dark olive brown at maturity. Spore wall continuous except for the occluded opening, consisting of three layers: A rigid, yellow-brown to red-brown outer wall 2-4 μ thick, and two hyaline inner membranes, the innermost sometimes minutely roughened; in older specimens wall at times becoming minutely perforate and the outer surface sloughing away. Spore contents globose to somewhat polygonal (reticulate in optical section). Hypha below spore attachment giving rise to many slender branches 1-2.5 μ diam. Vesicles in vesicular-arbuscular mycorrhizae thin-walled and lobed.

DISTRIBUTION, HABITAT, AND SEASON: Abundant from the coast of northern California to Washington to east of the Cascade Range in Oregon and Washington to elevations of 2,500 m, in dune sands, fields, pastures, and forests. Wet-sieved from soils collected throughout the year. Spores develop abundantly in pot culture 3½-4½ months. Also reported (as "honey-coloured sessile *Endogone* spores") from Florida (Schenck and Hinson, 1971), Australia and New Zealand (Mosse and Bowen, 1968a), Pakistan (Khan, 1971), and Scotland (as "spore type 6," Gerdemann and Nicolson, 1963).

MYCORRHIZAL ASSOCIATIONS: Forming vesicular-arbuscular endomycorrhizae with thin-walled, lobed vesicles. Associated in field collections with roots of *Chamaecyparis lawsoniana*, *Dactylis glomerata* L.,



*Thuja plicata*, *Bellis perennis* L., *Festuca* spp., *Fragaria* spp., *Hypochaeris radicata*, *Lupinus littoralis* Dougl. ex Lindl., *Phleum pratense* L., *Plantago* sp., *Stellaria* sp., and *Trifolium* spp. and forming endomycorrhizae in pot culture with *Allium cepa*, *Lycopersicon esculentum*, and *Zea mays*.

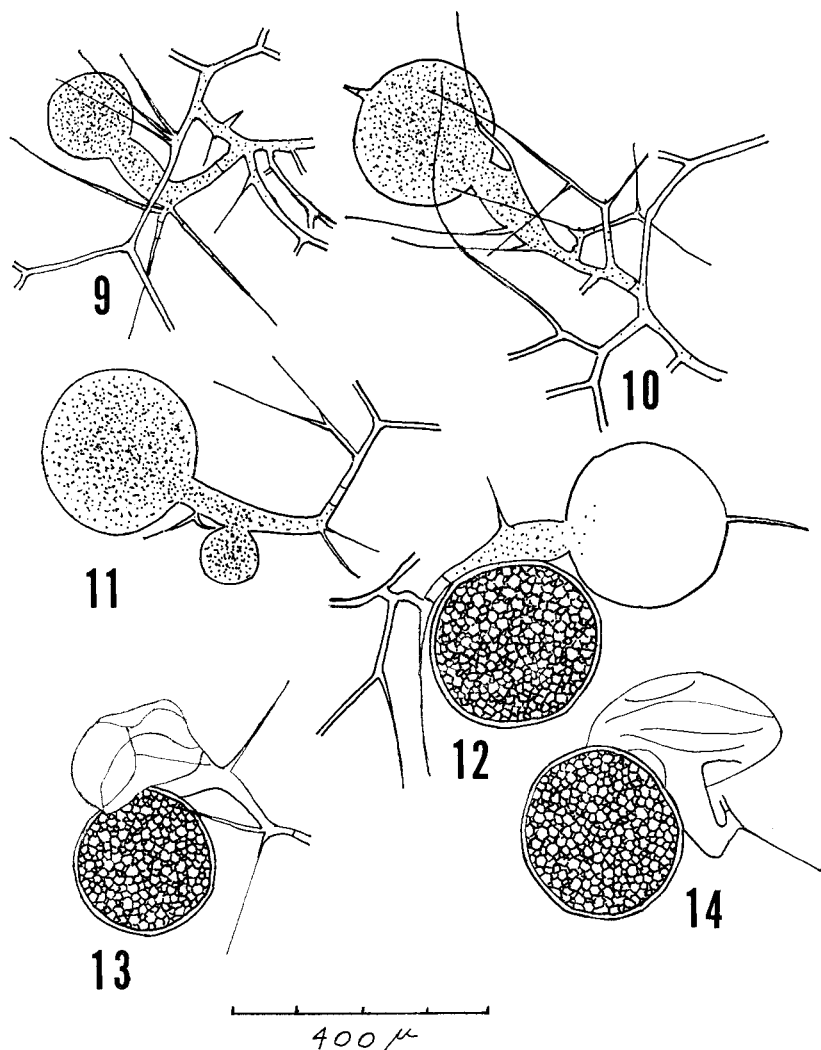
ETYMOLOGY: Latin, *laevis* (smooth), referring to the spore surface.

COLLECTIONS EXAMINED: TYPE: OREGON—*Benton Co.*: North-east foot of Mary's Peak along Woods Creek in abandoned field with weeds between the creek and the road; soil collected 6 October 1969, Trappe 2085 (OSC). PARATYPES: CALIFORNIA—*Mendocino Co.*: leg. Iwan Ho, Trappe 3119, 3122 (OSC). OREGON—*Baker Co.*: leg. Iwan Ho, Trappe 3256 (OSC). *Benton Co.*: Trappe 2101 (OSC); leg. Iwan Ho, Trappe 2154, 2162, 2209, 2230 (OSC). *Clatsop Co.*: leg. Iwan Ho, Trappe 3154 (OSC). *Coos Co.*: leg. Iwan Ho, Trappe 2589, 2590, 2611 (OSC). *Curry Co.*: leg. Iwan Ho, Trappe 2557 (OSC). *Deschutes Co.*: Trappe 2100 (OSC). *Josephine Co.*: leg. Iwan Ho, Trappe 3124 (OSC). *Lane Co.*: leg. Iwan Ho, Trappe 2225, 2592, 2881 (OSC). *Lincoln Co.*: leg. Iwan Ho, Trappe 2547, 2552, 2562, 2563, 2806 (OSC). *Tillamook Co.*: leg. Iwan Ho, Trappe 2539, 2596 (OSC). *Wasco Co.*: leg. Iwan Ho, Trappe 3200 (OSC). WASHINGTON—*Chelan Co.*: Trappe 1986, 2267, 3125 (OSC). *Clallam Co.*: leg. Iwan Ho, Trappe 3146 (OSC). *Grays Harbor Co.*: leg. Iwan Ho, Trappe 3142 (OSC). *Island Co.*: leg. Iwan Ho, Trappe 3148 (OSC). *King Co.*: leg. Iwan Ho, Trappe 3140 (OSC). *Pierce Co.*: Mt. Rainier National Park, Trappe 3049 (OSC). *Skagit Co.*: leg. Iwan Ho, Trappe 3149 (OSC).

### 18. *Acaulospora elegans* Trappe & Gerdemann, sp. nov.

Sporocarpia ignota. Sporae singillatim in terra enatae, sessiles, lateraliter gestae in hypha 40–60  $\mu$  diametro tunicis pallide brunneis 1–3  $\mu$  crassis vestita in vesiculam ellipsoideam vel globosam prope terminata. Vesiculae 150–240  $\mu$  diametro tunicis pallide brunneis 1–3  $\mu$  crassis vestitae, sporis maturis vacuae, contractae, plerumque e spora separatae. Sporae 140–285  $\times$  145–330  $\mu$ , globosae vel subglobosae, ellipsoideae, vel reniformes, surde obscure brunnae, superficie spinis spissis pallide brunneis 2  $\times$  0.5  $\mu$  ornatae, et mox reticulo alveoliformi e lamellis hyalinis 5–6  $\times$  1  $\mu$  composito spinis superimposito, plerumque completo sed in sporarum nonnullarum areolis haud formato, alveolis 4–8  $\mu$  longis. Sporarum tunicae continua, poro ocluso excepto, lamina exteriori brunnea ad 12  $\mu$  (spinis lamellisque inclusis) crassa, laminae tres hyalinas, cunctas usque ad 15  $\mu$  crassas, includente. Sub loco colligationis sporae hypha longe vel abrupte attenuata, hyphas multas abunde ramosas angustas proferens.

Sporocarps unknown. Spores forming singly in soil, sessile, borne laterally on a hypha 40–60  $\mu$  diam having pale brown walls 1–3  $\mu$  and terminating nearby in an ellipsoid to globose vesicle. Vesicles 150–240  $\mu$  diam with pale brown walls 1–3  $\mu$  thick, becoming empty and shrunken at spore maturity and usually detaching from the spore. Spores 140–285  $\times$  145–330  $\mu$ , globose to subglobose, ellipsoid or reniform, dull,



FIGS. 9-14. Developmental stages in the formation of azygospores of *Acaulospora laevis*. 9-10. Formation of the terminal vesicle. 11. Young azygospore budding laterally from stalk of vesicle. 12. Vesicle nearly empty of contents as azygospore matures. 13-14. Mature azygospores attached to empty collapsed vesicles.

dark brown; surface ornamented with crowded, light brown spines  $2 \times 0.5 \mu$ , soon developing an alveolate reticulum of hyaline ridges  $5-6 \times 1 \mu$  superimposed on the spines, reticulum generally complete but lacking on parts of the surfaces of occasional spores, alveoli  $4-8 \mu$  long. Spore wall continuous except for the occluded opening, the outer layer brown,

up to 12  $\mu$  thick (including spines and ridges), enclosing 3 hyaline walls which total up to 15  $\mu$  thick. Hypha below spore attachment long-tapered to abruptly attenuated, giving rise to many, frequently branched, narrow hyphae.

**DISTRIBUTION, HABITAT, AND SEASON:** Widely distributed in coastal sands of northern California to southwestern Washington; one collection is known from a road bank on the east slope of the Oregon Coast Range and one from a landscaped area of the Willamette Valley. Spores have been sieved from field samples essentially throughout the year.

**MYCORRHIZAL ASSOCIATIONS:** Associated with endomycorrhizae of *Epilobium angustifolium* L., *Festuca* sp., *Fragaria chiloensis*, *Hypochaeris radicata*, and *Thuja plicata* in the field.

**ETYMOLOGY:** Latin, *elegans* (elegant), referring to the complex and attractive spore ornamentation.

**COLLECTIONS EXAMINED:** TYPE: OREGON—*Tillamook Co.*: Sand Lake Campground among roots of *Fragaria chiloensis* in dune sand, 3 September 1970, Trappe 2220 (OSC). PARATYPES: CALIFORNIA—*Humboldt Co.*: leg. Iwan Ho, Trappe 3118 (OSC). *Mendocino Co.*: leg. Iwan Ho, Trappe 3120 (OSC). OREGON—*Benton Co.*: leg. Iwan Ho, Trappe 2269, 2574 (OSC). *Coos Co.*: leg. Iwan Ho, Trappe 2593, 2595, 2613 (OSC). *Lane Co.*: leg. Iwan Ho, Trappe 2578, 2591 (OSC). *Lincoln Co.*: leg. Iwan Ho, Trappe 2549, 2551, 2554, 2560 (OSC). WASHINGTON—*Clallam Co.*: leg. Iwan Ho, Trappe 3145 (OSC). *Pacific Co.*: leg. Iwan Ho, Trappe 3156 (OSC).

The surface ornamentation of *A. elegans* is equaled in complexity and elegance only by that of an unnamed *Gigaspora* sp. from Nigeria (Old et al., 1973).

#### IV. GLOMUS Tul. & Tul., Giorn. Bot. Ital. 2 (Pt. 1): 63. 1845.

*Type species: Glomus microcarpus* Tul. & Tul.

*Endogone* p. p.

*Sphaeroceas* Sacc. & Ellis, *Michelia* 8: 582. 1882.

?*Rhizophagus* Dangeard, *Le Bot.* 5: 38–43. 1896. *Illus., Le Bot.* 7: P18–9. 1900.

?*Stigeosporium* West, *Ann. Bot.* 30: 357. 1916.

*Rhizophagites* Rosendahl, *Bull. Torrey Bot. Club* 70: 131. 1943.

Chlamydospores borne terminally on single (rarely two) undifferentiated, nongametangial hyphae in sporocarps or individually in soil. Spore contents at maturity separated from attached hyphae by a septum or occluded by spore wall thickening.

**ETYMOLOGY:** Latin, *glomus* (a ball of yarn), possibly in reference to the sometimes rounded and cottony appearance of the species for which the Tulasnes erected the genus.

Some species are known only from sporocarps, while others produce loose open clusters of spores and isolated single spores as well as sporocarps. One variety of *Glomus macrocarpus* Tul. & Tul. is known only to form single spores.

Chlamydospore germination in all species in which it has been observed is by renewed growth from subtending hyphae (Mosse, 1956, 1959; Godfrey, 1957c). Smaller spores occasionally form within chlamydospores, a phenomenon of unknown significance. In one species, *G. radiatus* (Thaxter) Gerd. & Trappe, the chlamydospores usually fill with glebal hyphae.

It has generally been assumed that the chlamydosporic species represent asexual stages of zygosporic species; however, beyond the general resemblance of sporocarps and spores, there is little good evidence for such a relationship. Thaxter (1922) found groups of zygosporic spores associated with chlamydospores in sporocarps of *G. fasciculatus* (Thaxter) Gerd. & Trappe. However, there is substantial doubt that the chlamydospores and zygosporic spores in this collection belong to the same species (Gerdemann, 1965). These sporocarps are loose structures that incorporate sphagnum and other foreign matter, and the hyphae attached to chlamydospores are thick-walled, while hyphae associated with the zygosporic spores are thin-walled. Quite possibly this collection consists of a mixture of two species. *Glomus fasciculatus* has been maintained in pot culture for many years and only chlamydospores have formed. Godfrey (1957a) described a single sporocarp of *G. microcarpus* that contained both zygosporic spores and chlamydospores, suggesting a link between the chlamydosporic and zygosporic species. We examined a permanent mount of this specimen, kindly loaned by Professor L. E. Hawker. Godfrey noted that the zygosporic spores were borne in dark orange patches interspersed in the cream-colored chlamydospore-bearing tissue. Also, in the prepared microslide we noted that the hyphae associated with the two kinds of spores appear to differ. This suggests a freak combination of two species growing together in a single sporocarp or possibly hyperparasitism. No similar phenomenon has been observed in *G. microcarpus* by us or reported elsewhere. The apparent absence of zygosporic species from grasslands and cultivated soils, where the chlamydosporic species are especially prevalent, is evidence that chlamydosporic species are not asexual stages of zygosporic species.

There is good experimental evidence that a number of *Glomus* species produce endomycorrhizae with vesicles and arbuscules. Several additional species have been found closely associated with endomycorrhizae, and very likely most, if not all, *Glomus* spp. produce vesicular-arbuscular mycorrhizae. This most common type of mycorrhiza occurs on more plant species than any other type. It occurs on nearly all crop plants, ornamentals, and wild herbaceous plants, as well as many shrubs and trees. Numerous experiments with *Glomus* species have shown that

the mycorrhizal infections increase nutrient and moisture uptake and improve plant growth (Gerdemann, 1968, 1970; Safir et al., 1971).

*Glomus* species are found in most habitats in nature. They are very common in cultivated soils and widespread in native grasslands and forests. In fact, they may very well be the most common of all soil-borne fungi. Reported associations with ectomycorrhizal tree hosts are open to question. In most cases the collectors did not carefully note whether endomycorrhizal hosts such as grasses or other herbaceous plants were also present.

Fruiting in this genus is most often hypogeous, although sporocarps of some species occur on sphagnum, on the soil surface, or on rotten wood or other detritus. Sporocarps are generally found by raking the upper soil surface, whereas spores and small sporocarps have been collected by wet-sieving and decanting. The pot inoculation technique is useful for obtaining species from soils too high in organic matter to sieve.

Species in this group are easily maintained in open pot cultures. However, they cannot readily be obtained in axenic culture. Surface sterilized spores of *G. mosseae* (Nicol. & Gerd.) Gerd. & Trappe have germinated and produced hyphal growth on various culture media (Mosse, 1959); however, such growth could not be maintained and hyphae could not be subcultured. Mosse (1962) obtained pure cultures of *G. mosseae* with various host plants growing on agar media; however, the fungus could not be subcultured without a living host. It is likely that Barrett's (1961) "*Rhizophagus* cultures" obtained by a complex hemp-seed-baiting technique were members of this group. An isolate obtained from a sporocarp of *G. mosseae* by use of Barrett's method closely resembled his "*Rhizophagus* cultures" (Gerdemann, 1968). However, since the culture did not produce spores and attempts to synthesize mycorrhiza with it consistently failed, it is not certain whether the isolated fungus was *G. mosseae* or a contaminant.

We consider *Rhizophagus* to be a probable synonym of *Glomus*. Dangeard's excellent illustrations of vesicles and arbuscules leave little doubt that he described a mycorrhiza formed by a *Glomus* species. Butler (1939) transferred the one species described for *Stigeosporium* to *Rhizophagus*. Since West's (1916) description is highly suggestive of a *Glomus* type mycorrhiza we have also listed *Stigeosporium* as a probable synonym of *Glomus*. Rosendahl (1943) described and illustrated his fossil genus, *Rhizophagites*, in detail; it is clearly synonymous with *Glomus*.

#### KEY TO THE SPECIES OF GLOMUS

1. Globose spores in a collection less than 50  $\mu$  diam (nonglobose spores usually also present and may be longer than 50  $\mu$ ) ..... 2
1. Globose spores regularly exceeding 50  $\mu$  diam ..... 3

2. Sporocarps sparsely pubescent with prominent, erect, pointed aggregations of white hyphae; spore attachment thin-walled, hyaline, inconspicuous; epigeous on rotten wood or other detritus ..... 30. *G. pubescens*
2. Spores ectocarpic or in sporocarps; sporocarp surfaces lacking erect, pointed hyphal aggregations; spore attachment conspicuous; hypogeous ..... 25. *G. microcarpus*
3. Spore base funnel-shaped above the attachment; spores ectocarpic or borne in sporocarps with 1-10 spores enclosed in a peridium .... 19. *G. mosseae*
3. Spore base not funnel shaped ..... 4
4. Sporocarps of 1-2(-3) spores enclosed in a peridium, or single spores naked to partially enclosed; spore surface often minutely echinulate ..... 20. *G. monosporus*
4. Sporocarps with many spores, or spores ectocarpic; spore surface smooth or appearing roughened from adherent debris, never echinulate 5
5. Spores dark brown to brownish black, in sporocarps that exude a copious, cream-colored latex when cut fresh; spore wall a single layer, dark brown at exterior, grading to hyaline near inner surface ..... 22. *G. melanosporus*
5. Sporocarps present or absent, when present not exuding latex; spore walls with one or more layers, each layer uniform in color ..... 6
6. Spores formed in sporocarps in distinct to obscure radiate rows, the most mature spores at the sporocarp base and the youngest at the outer surface ..... 23. *G. radiatus*
6. Spores not in radiate rows ..... 7
7. Sporocarps containing many spores, each tightly enclosed in a hyphal mantle ..... 21. *G. convolutus*
7. Spores not enclosed in a hyphal mantle ..... 8
8. Sporocarps containing thick-walled spores overlain by a peridium-like layer of elongate, thin-walled vesicles up to  $152 \times 103 \mu$  .. 24. *G. vesiculifer*
8. Sporocarps, if present, lacking large vesicles (smaller, inflated cells may be present) ..... 9
9. Groups of spores budding from all sides and the apex of enlarged, thick-walled, hyphal terminations to form rounded spore clusters within sporocarps (extralimital species) ..... 31. *G. fuegianus*
9. Spores formed individually and terminally as hyphal end cells in sporocarps or ectocarpically in soil ..... 10
10. Many spores in a collection globose to subglobose ..... 11
10. Spores ellipsoid to obovoid (or occasionally some in a given collection subglobose) ..... 16
11. Globose spores  $35-105 \mu$  diam ..... 12
11. Globose spores mostly exceeding  $100\mu$  diam at maturity and generally exceeding  $120 \mu$  ..... 14
12. Spore walls  $3-17 \mu$  thick; hyphal attachment at maturity occluded by spore wall thickening; usually hypogeous ..... 26. *G. fasciculatus*
12. Spore walls  $2.5-4(-5) \mu$  thick; hyphal attachment closed by a thin septum at point of attachment; epigeous on sticks or litter, tropical .... 13
13. Spores  $65-82(-100) \times 65-90(-105) \mu$ ; hyphal attachments  $10-15$  diam (extralimital species) ..... 36. *G. pulvinatus*
13. Spores  $53-73 \times 49-62 \mu$ ; hyphal attachments  $6-9(-13) \mu$  diam (extralimital species) ..... 37. *G. fragilis*
14. Spore with a smooth, hyaline, easily separable (under pressure) outer wall  $1-4(-8) \mu$  thick and a yellow to brown inner wall  $4-8(-10) \mu$  thick ..... 29. *G. caledonius*
14. Spore lacking a readily separable outer wall ..... 15
15. Spore walls yellow to brown; subtending hyphae with walls thin or thickened for a distance of  $10-50(-100) \mu$ , if thickened then spores often

- with a thin, adherent, hyaline outer wall; spores borne in sporocarps or open clusters ..... 27. *G. macrocarpus* var. *macrocarpus*
15. Spore walls dark brown to near black, lacking a thin, hyaline outer wall; subtending hyphae with brown walls thickened for a distance of 50–150  $\mu$ ; spores ectocarpic in soil. .... 28. *G. macrocarpus* var. *geosporus*
16. Spores 149–230  $\mu$  long (extralimital species) ..... 32. *G. flavisporus*
16. Spore length 145  $\mu$  or less ..... 17
17. Spores 125–145  $\times$  100–110 $\mu$ ; walls reddish brown, up to 8  $\mu$  thick (extralimital species) ..... 33. *G. borealis*
17. Spores 70–120(–160)  $\times$  50–80  $\mu$ ; walls yellow, 4–5  $\mu$  thick ..... 18
18. Spores 70–100  $\times$  54–70  $\mu$ ; hyphal attachment 4–6  $\mu$  broad (extralimital species) ..... 34. *G. canadensis*
18. Spores 70–120(–160)  $\times$  50–80  $\mu$ ; hyphal attachment 8–15  $\mu$  broad, tropical (extralimital species) ..... 35. *G. fulvus*
19. **Glomus mosseae** (Nicol. & Gerd.) Gerdemann & Trappe, comb. nov.

=*Endogone mosseae* Nicol. & Gerd., Mycologia 60: 314–315. 1968.

Sporocarps 1–10 spored, globose to ellipsoid, up to 1 mm diam. Peridium of loosely interwoven, irregularly branched, hyaline, septate hyphae 2–12  $\mu$  diam, the walls up to 0.5  $\mu$  thick, frequently anastomosing to form a thin network, enclosing the chlamydospores entirely, incompletely or with some spores unenclosed. Endocarpic and ectocarpic spores similar. Chlamydospores yellow to brown, globose to ovoid, obovoid, or somewhat irregular, 105–310  $\times$  110–305  $\mu$ , with one or occasionally two funnel-shaped bases 20–30(–50)  $\mu$  diam, divided from subtending hyphae by a curved septum; walls 2–7  $\mu$  thick, with a thin, often barely perceptible hyaline outer membrane, and a thick, brownish-yellow inner layer.

DISTRIBUTION, HABITAT, AND SEASON: Hypogeous, widespread in the Pacific Northwest, from coastal dune sands to mountain forests and semi-arid zones; especially common in alkaline flats, fields, roadbanks, and forest clearings. Collected in the field throughout the year. Also reported from Illinois, England, Scotland, and Germany (Nicolson and Gerdemann, 1968), Australia, New Zealand, and Pakistan as “yellow vacuolate spores” (Mosse and Bowen, 1968a; Khan, 1971). We have also found it in a soil sample from Hawaii (cited below).

MYCORRHIZAL ASSOCIATIONS: Forming vesicular-arbuscular mycorrhizae with a wide diversity of plants. In the Pacific Northwest found associated in the field with mycorrhizae of *Chamaecyparis lawsoniana*, *Agropyron* sp., *Allium cepa*, *Avena fatua* L., *Bellis perennis*, *Dactylis glomerata*, *Distichlis* sp., *Epilobium angustifolium* L., *Festuca* sp., *Fragaria* spp., *Helianthus annuus* L., *Lolium* sp., *Mentha arvensis* L., *Plantago* sp., *Poa* sp., *Potentilla* sp., *Trifolium* spp., and *Triticum aestivum*, and forming endomycorrhizae in pot culture with *Allium cepa*,

*Fragaria vesca* L., *Sambucus caerulea* Raf., *Triticum aestivum*, and *Zea mays*.

ETYMOLOGY: Named in honor of Dr. Barbara Mosse, the discoverer of the species and long-time student of the Endogonaceae.

COLLECTIONS EXAMINED: ALASKA—Near Fairbanks, leg. T. Chapin, Trappe 3497 (OSC). CALIFORNIA—*Sierra Co.*: leg. A. E. Gilmore, Trappe 2171 (OSC). *Yolo Co.*: A. E. Gilmore E2, E4 (OSC). HAWAII—*Oahu*: Trappe 2548 (OSC). OREGON—*Baker Co.*: leg. Iwan Ho, Trappe 3257 (OSC). *Benton Co.*: leg. Iwan Ho, Trappe 2205, 2218, 2236, 2270, 2531, 2537, 2585, 2734 (OSC). *Coos Co.*: leg. Iwan Ho, Trappe 2607, 2609, 2610 (OSC). *Curry Co.*: leg. Iwan Ho, Trappe 2564 (OSC). *Deschutes Co.*: Trappe 2422 (OSC). *Harney Co.*: leg. Iwan Ho, Trappe 3507, 3512, 3514, 3515 (OSC). *Jefferson Co.*: leg. Iwan Ho, Trappe 3201 (OSC). *Morrow Co.*: leg. Iwan Ho, Trappe 3266 (OSC). *Tillamook Co.*: Trappe 2884 (OSC). *Umatilla Co.*: leg. Iwan Ho, Trappe 3252, 3264 (OSC). *Union Co.*: leg. Iwan Ho, Trappe 3253 (OSC). *Wasco Co.*: leg. Iwan Ho, Trappe 3198, 3199 (OSC). WASHINGTON—*Asotin Co.*: leg. Iwan Ho, Trappe 2265, 3064 (OSC). *Chelan Co.*: leg. W. Fisher and C. Stevens, Trappe 2917 (OSC). *Okanogan Co.*: Trappe 2214 (OSC). *San Juan Co.*: leg. Iwan Ho, Trappe 3152 (OSC).

Chlamydo-spores with unusually large, funnel-shaped bases are often obtained in the Northwest. The bases range from 25–50  $\mu$  in width near the spore and are from 35–60  $\mu$  long. A septum in the neck of the funnel separates the spore contents from the sporophore. These spores appear somewhat intermediate between typical spores of *G. mosseae* and those produced by a species ("funnel-shaped spores") found by Mosse and Bowen (1968a) in Australia. Other sporocarps obtained from the same soil samples have often contained chlamydo-spores typical for *G. mosseae*. The occurrence of these two types of spores together, often with intermediate specimens, precludes erection of a separate taxon for the nontypical spores until a consistent difference can be demonstrated.

## 20. *Glomus monosporus* Gerdemann & Trappe, sp. nov. FIG. 15

Sporocarpia 150–452  $\times$  169–470  $\mu$ , globosa vel ellipsoidea, chlamydo-sporam plerumque unam continens, interdum duas, raro tres. Peridium e hyphis ramosis, tenuiter tunicatis, intimis 4–10  $\mu$  diametro maturitate, superficialibus 1.5–2.5  $\mu$ , e hyphis sustentantibus prope sporae basim evolventibus, plerumque multas soli particulas includentibus, evolutione variabilibus, intertextum, sporis vel omnino inclusis, obscuratis vel inclusis tamen conspicuis vel ab hyphis paucis prope basim partim inclusis vel sine ullis hyphis includentibus. Chlamydo-sporae 140–330  $\mu$  diametro, plerumque globosae vel subglobosae, raro ellipsoideae. Sporae tunica 4–10  $\mu$  crassa, surde brunnea, e lamina externa tenui frequenter detersa et interna crassa composita, interna laminata, aculeis minutis, crebris vel dispersis in ex-



ternam protrusis notata, incrassatione ejus in hypham subtendentem producta. Hyphae subtendentes 8–12  $\mu$  diametro, plerumque valde recurvatae et ad sporae tunicam appressae, nonnumquam binae. Sporae globulos oleosos continentes vel interdum hyphis tenuiter tunicatis 3–6  $\mu$  diametro completatae.

Sporocarps 150–452  $\times$  169–470  $\mu$ , globose to ellipsoid, containing mostly 1, occasionally 2, or rarely 3 chlamydospores. Peridium of branched, interwoven, thin-walled hyphae, the innermost 4–10  $\mu$  diam, the surface hyphae 1.5–2.5  $\mu$  diam at maturity, developing from subtending hypha at spore base, usually incorporating many soil particles, degree of development variable: spores completely enclosed and obscured to enclosed but visible, partially enclosed, with only a few hyphae near base, or without any enclosing hyphae. Chlamydospores 140–330  $\mu$  diam, generally globose to subglobose or rarely ellipsoid. Spore walls 4–10  $\mu$  thick, dull brown, composed of a thin outer wall which often flakes off and a thick inner wall; inner wall laminate, with minute, abundant to scattered echinulations that protrude into the outer wall; thickening of inner wall extending into subtending hypha. Subtending hyphae 8–12  $\mu$  diam, generally strongly recurved and appressed to spore walls. Chlamydospores occasionally with 2 subtending hyphae. Spores containing oil globules or occasionally filled with hyaline, thin-walled hyphae 3–6  $\mu$  diam.

DISTRIBUTION, HABITAT, AND SEASON: Northwestern Oregon to northwestern Washington from near the coast to the Willamette Valley and Puget Sound area in forests, fields, and greenhouses. Collected in the field, August through March. Probably present in soil throughout the year.

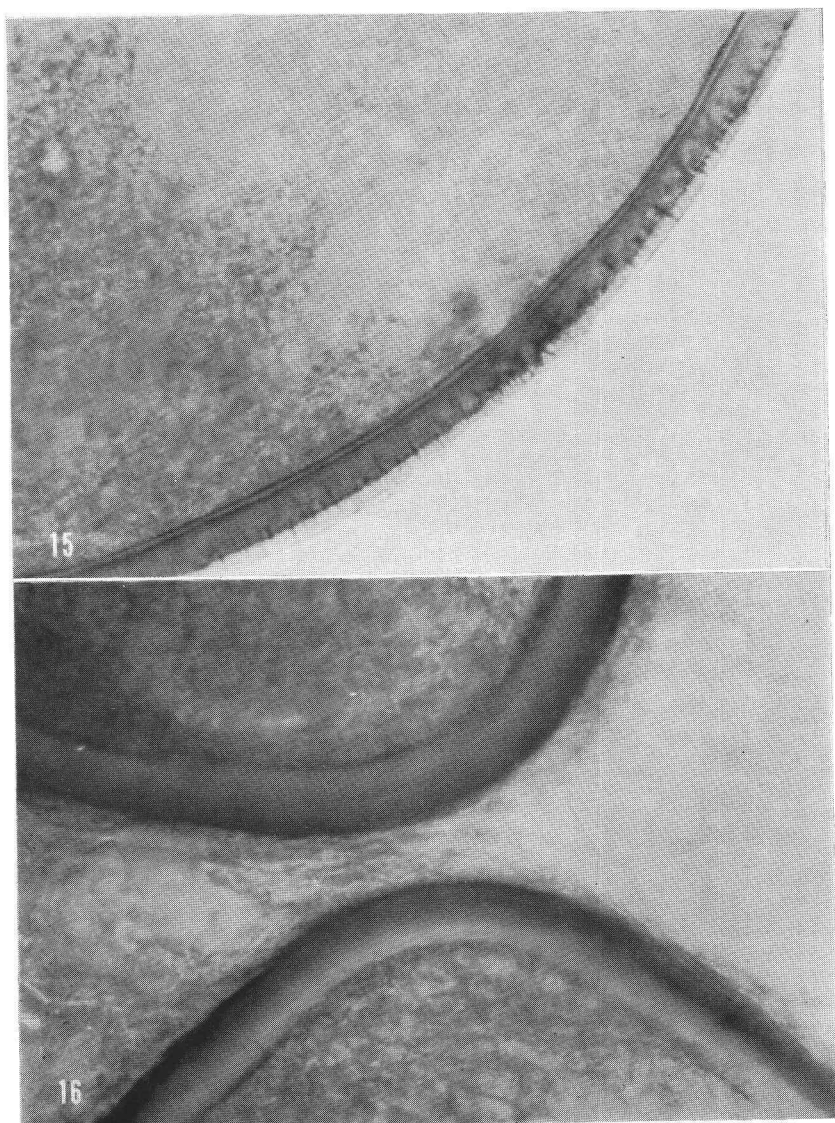
MYCORRHIZAL ASSOCIATIONS: Forming vesicular-arbuscular mycorrhizae. Associated in the field with endomycorrhizae of *Bellis perennis*, *Chamaecyparis lawsoniana*, *Hypochaeris radicata*, and *Triticum aestivum*, and forming mycorrhizae in pot culture with *Bellis perennis*, *Lycopersicon esculentum*, *Maianthemum dilatatum* (Wood) Nels. & Macbr., *Trillium ovatum* Pursh, and *Zea mays*.

ETYMOLOGY: Greek, *mono-* (one) and *-sporus* (spore), referring to the usually one-spored sporocarps.

COLLECTIONS EXAMINED: TYPE: OREGON—*Benton Co.*: Oregon State University, southeast corner of Forestry Sciences Laboratory parking lot, from around roots of grasses and *Trifolium repens* L., 18 December 1969, Trappe 2089 (OSC). PARATYPES: OREGON—*Benton Co.*: leg. Iwan Ho, Trappe 2151, 2164, 2208, 2221, 2534 (OSC). *Coos Co.*: leg. C. Maser, Trappe 3204 (OSC). *Lincoln Co.*: Trappe 2224 (OSC). *Linn Co.*: Trappe 2266 (OSC). WASHINGTON—*King Co.*: leg. Iwan Ho, Trappe 3153 (OSC). *San Juan Co.*: leg. Iwan Ho, Trappe 3150 (OSC).

21. *Glomus convolutus* Gerdemann & Trappe, sp. nov. Fig. 17

Sporocarpia 2–9 mm crassa maxime lobata, convoluta, involuta, irregulariaque, verrucosa, dura fragiliaque, uda splendide crocea, vel aurantiaco-crocea, sicca pal-



FIGS. 15-16. Chlamyospore wall structure in *Glomus*,  $\times 625$ . 15. *Glomus monosporus*, showing the thin outer-wall, and the thicker inner-wall with minute echinulations projecting into the outer-wall. 16. *Glomus melanosporus*, showing the gradation in color from dark reddish-brown at the surface to subhyaline near the inner surface.

lide aurantiaco-crocea, nonnumquam materiam alienam aliquantam retinentia. Nullum peridium. Gleba fere 2 mm crassa, chlamydosporas globosas vel ovatas  $81-193 \times 67-193 \mu$  singillatim inclusas in palla  $5-50 \mu$  crassa ex hyphis tenuiter tunicatis intertextis  $1.5-5 \mu$  latis composita continens. Sporae recentes globulis vivide luteis oleosis suffultae, facile inter se separabiles, pallis tamen difficilibus demotu, sporarum tunica  $8-15 \mu$  crassa, laminata, pallide crocea in liquore lactophenolico, in liquore iodico Melzeri sature aurantiaco-brunnea, crassificatione per spatium parvum in hyphas sustentantes extensa.

Sporocarps 2-9 mm broad, much lobed, convoluted, infolded, and irregular, verrucose, hard and brittle, bright orange to orange-yellow when moist, light orange to yellow when dry, at times with some adhering debris. Peridium absent. Gleba approximately 2 mm thick. Sections of fresh specimens in Melzer's solution having localized clusters of green to black granules within hyphae and within and adhering to oil globules exuded from cut hyphae (granules scarce to absent in revived specimens). Chlamydo-spores  $81-193 \times 67-193 \mu$ , globose to obovoid, each spore tightly enclosed in a mantle  $5-50 \mu$  thick of intertwined, thin-walled hyphae  $1.5-5 \mu$  broad. Spores filled with deep yellow oil globules when fresh, readily separating from each other, but mantles removable only with difficulty. Spore wall  $8-15 \mu$  thick, laminate, hyaline to light yellow in lactophenol, deep orange brown in Melzer's solution. Hyaline wall thickening extending a short distance into the subtending hypha. Hyphal attachment  $6-13 \mu$  diam.

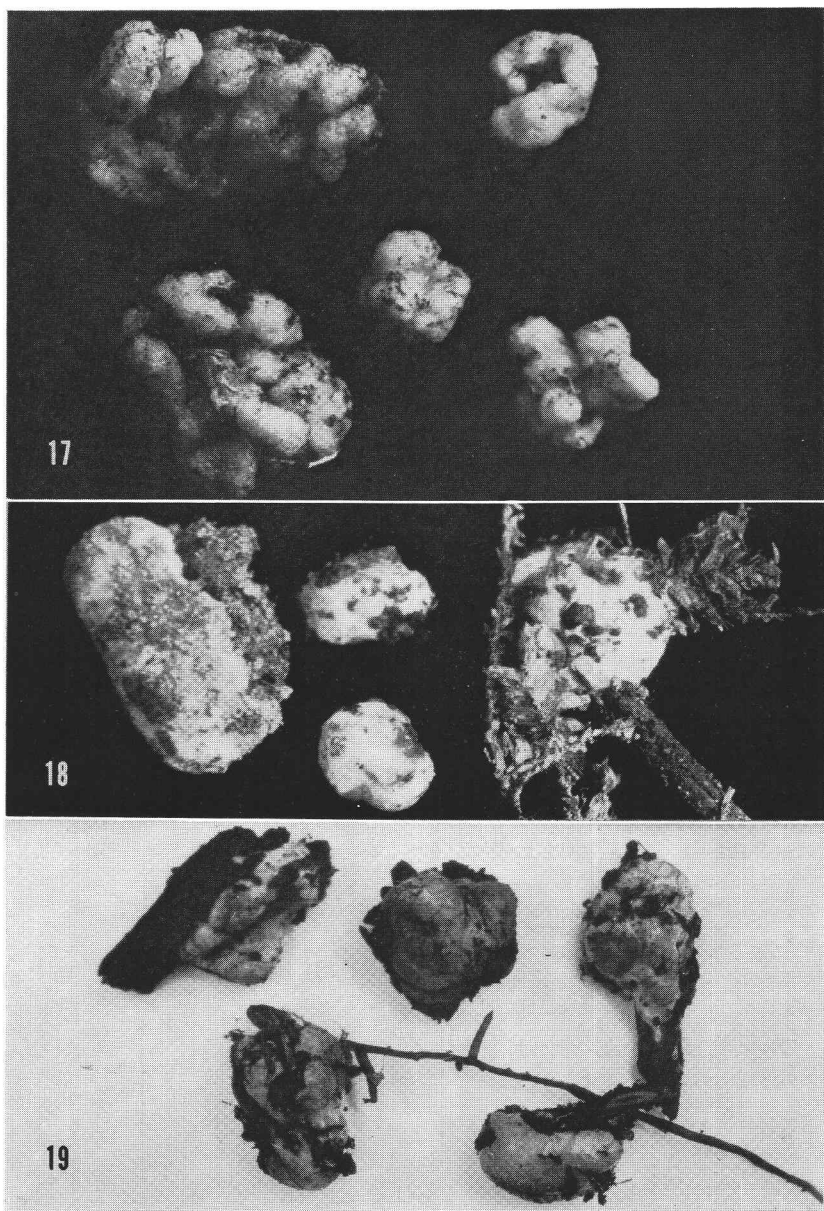
DISTRIBUTION, HABITAT, AND SEASON: Hypogeous or epigeous in the Cascade Mountains of Washington and Oregon to the Siskiyou Mountains in northern California, and east to the Bitterroot Mountains of Montana, on soil or conifer needles and rotted wood near or under the edges of melting snowbanks, June to August.

MYCORRHIZAL ASSOCIATIONS: Unknown; this species may be a facultative saprophyte or a parasite on other fungi.

ETYMOLOGY: Latin, *convolutus* (convolute), referring to the form of the sporocarp.

COLLECTIONS EXAMINED: TYPE: CALIFORNIA—*Del Norte Co.*: Siskiyou Mountains, Sanger Lake, elev. ca. 1,500 m, at edge of melting snowbank in absence of any ground vegetation, 29 June 1971, Trappe 2778 (OSC). PARATYPES: MONTANA—*Granite Co.*: Trappe 3656 (OSC). OREGON—*Lane Co.*: Trappe 2847 (OSC). WASHINGTON—*Lewis Co.*: Trappe 1987 (OSC). *Pierce Co.*: Mt. Rainier Nat. Park, A. H. Smith 29022 (MICH), 29120 (MICH, OSC). *Skamania Co.*: Trappe 1862 (OSC).

This species is often found in the same snowbank habitat and at the same season that characterizes many spring collections of *Endogone pisiformis*. The two species have been found in mixture, and since they are approximately the same size and color, they can be confused. They are readily separable with a hand lens or stereomicroscope. *G. convolutus* is usually much more lobed and convoluted and more deeply orange hued than *E. pisiformis*. Also, the sporocarps of *E. pisiformis*



FIGS. 17-19. Sporocarps of *Glomus*. 17. *Glomus convolutus*,  $\times$  4.3. 18. *Glomus macrocarpus*,  $\times$  4.2. 19. *Glomus radiatus*, showing the attachment of one sporocarp to a root of *Chamaecyparis nootkatensis*,  $\times$  2.9.

are enclosed in a peridium. No peridium encloses the sporocarp of *G. convolutus*, but each spore is enclosed in a hyphal mantle.

22. *Glomus melanosporus* Gerdemann & Trappe, sp. nov. FIG. 16

Sporocarpia ovata,  $8 \times 12 \times 12$  mm, sine peridio, superficie e hyphis albis laxis cum chlamydosporis pallide brunneis vel obscure rubro-brunneis interspersis, secta laticem abundantem cremeum exudentia. Gleba brunneo-fusca chlamydosporas pallide brunneas, obscure rubro-brunneas, vel subfuscas  $166\text{--}227 \times 129\text{--}244 \mu$ , subglobosas, obovoideas, vel late ellipsoideas, inter hyphas crassas tenuiter tunicatas sitas, et paulum materiae alienae, continens. Sporarum tunica  $8\text{--}13 \mu$  crassa, laminata, matura e colore obscure rubro-brunneo apud superficiem externam ad pallide croceum vel subhyalinum apud internam desinens. Hyphae sustentantes crassae, tenuiter tunicatae, difficiles visu, ad spora basim  $15\text{--}20 \mu$  diametro, prope sporam ad  $25 \mu$  vel plus expansae.

Sporocarp ovate,  $8 \times 12 \times 12$  mm, peridium absent, surface with white loose hyphae interspersed with light brown to dark reddish-brown chlamydospores, exuding abundant creamy latex when cut. Gleba brownish-black, containing light-brown to dark reddish-brown or nearly black chlamydospores  $166\text{--}277 \times 129\text{--}244 \mu$ , subglobose to obovoid or broadly ellipsoid, embedded in coarse thin-walled hyphae, gleba also containing small quantities of foreign matter. Spore wall  $8\text{--}13 \mu$  thick, laminate, when mature grading in color from dark reddish-brown at the outer surface to light yellow or subhyaline near the inner surface. Subtending hypha coarse, thin-walled, difficult to observe,  $15\text{--}20 \mu$  diam at spore base, broadening to  $25 \mu$  or more a short distance from spore.

DISTRIBUTION, HABITAT, AND SEASON: Known only from the type collection; hypogeous.

MYCORRHIZAL ASSOCIATIONS: Unknown.

ETYMOLOGY: Greek, *melanosporus* (black spored), referring to the very dark spores that in mass render the gleba black.

COLLECTIONS EXAMINED: TYPE: OREGON—*Linn Co.*: Tombstone Pass, Tombstone Prairie, 26 June 1965, solitary in soil under *Abies amabilis* and herbs, Trappe 507 (OSC).

The nearly black gleba, the spores with walls that grade from dark colored near the outer surface to pale near the inner surface, and the exudation of latex from cut surfaces of fresh specimens readily differentiate this species from others in the genus *Glomus*.

23. *Glomus radiatus* (Thaxter) Trappe & Gerdemann, comb. nov.

FIGS. 19–22

≡ *Endogone radiata* Thaxter, Proc. Am. Acad. Arts Sci. 57: 316. 1922.

Sporocarps up to  $9 \times 7 \times 3$  mm, generally flattened and lobed, firm, attached to roots or organic matter, near white to grayish-yellow where

surface hyphae become matted. Peridium absent. Sporocarp developing acrogenously. Chlamydo-spores at or near the surface thin-walled and vesicular, becoming progressively thicker walled in the direction of the sporocarp base,  $60-110(-120) \times 48-75(-90) \mu$ , ellipsoid to oblong, obovoid or rarely globose, arranged in a distinct radial pattern, grouped or widely dispersed in a matrix of coarse thin-walled hyphae, usually containing hyphae similar to those in gleba. Spore wall  $4-8 \mu$  thick, laminate, light yellow. Subtending hyphae somewhat coarser than glebal hyphae, the opening into the spore up to  $6 \mu$  wide, only partially occluded by spore wall thickening but occluded by a plug below the spore base.

**DISTRIBUTION, HABITAT, AND SEASON:** Known in the Pacific Northwest from wet mountain soils (stream banks and hummocks in a boggy, montane meadow) in the Cascade Range of Oregon and Washington in October and November; hypogeous. Previously recorded from Maine, New Hampshire, and Quebec (Thaxter, 1922), and in a collection from New York examined by us.

**MYCORRHIZAL ASSOCIATIONS:** Associated in the field with endomycorrhizae of *Chamaecyparis nootkatensis* (D. Don) Spach. Thick-walled vesicles within the mycorrhizae were identical to chlamydo-spores in the sporocarps, except that most vesicles were not filled with hyphae.

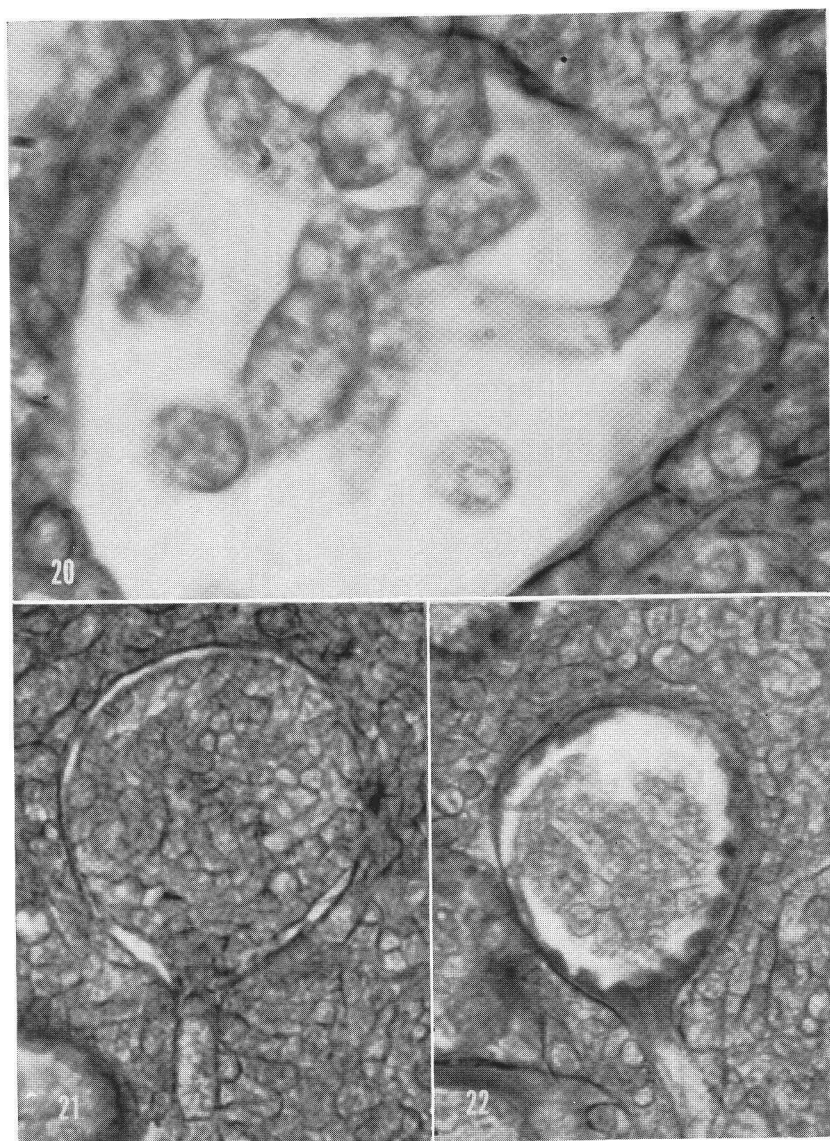
**ETYMOLOGY:** Latin, *radiatus* (radiate), referring to the radiate arrangement of spores from the sporocarp base.

**COLLECTIONS EXAMINED:** OREGON—*Lane Co.*: Trappe 2043 (OSC). WASHINGTON—*Lewis Co.*: Trappe 3449 (OSC).

These collections are very similar to those described by Thaxter from the Northeast. The western form differs only in having slightly larger spores with thicker walls. The striking radial arrangement of spores makes this a unique species. Acrogenous sporocarp development has been reported for one other chlamydo-spore species (Thaxter, 1922): *Glomus pubescens* (Sacc. & Ellis) Trappe & Gerdemann.

If sporocarps of *G. radiatus* are sectioned across rather than along the radiate alignment of spores, the spores in cross section will appear globose. In this case, very few hyphal attachments will be seen.

Chlamydo-spores filled with hyphae also occur in the following northeastern collections of *G. radiatus*: Thaxter 5187, 5188 (both FH) and 6323 (NY) and Gilkey 667 (OSC), collected near Ithaca, New York by D. P. Rogers, and M. Rosinsky, 5 September 1952. Spores in the type specimen (Thaxter 5189, FH) are apparently free of hyphae. The hyphae grow from the gleba through the thin walls of very young spores. As spores mature, the thickening walls cut across these penetrating hyphae and ultimately completely separate the hyphae within the spore from those of the gleba. Hyphae within spores closely resemble those in the gleba, and no evidence of parasitic fungi was found.



FIGS. 20-22. Chlamydospores of *Glomus radiatus*, containing hyphae. 20. Penetration of young thin-walled spores by hyphae from the gleba,  $\times 1340$ . 21. Chlamydospore with interior filled with hyphae. Note the resemblance of hyphae in spore to those in gleba,  $\times 604$ . 22. Mature spore. The uneven wall thickening is unusual,  $\times 604$ .

24. *Glomus vesiculifer* (Thaxter) Gerdemann & Trappe, comb. nov.

≡ *Endogone vesiculifera* Thaxter, Proc. Am. Acad. Arts Sci. 57: 309–310. 1922.

==? *Endogone tjibodensis* Boedj., Bull. Jard. Bot. Buitenzorg Ser. 3, 13: 504–505. 1935.

Sporocarp  $13 \times 10$  mm, forming a crust on soil surface, whitish, surface covered with a peridium-like layer of thin-walled vesicles up to  $152 \times 103 \mu$ , initially globose, becoming ellipsoid to broadly clavate and rounded at the tip, at times constricted near middle, whitish. Chlamydo-spores produced in tubercles, globose or subglobose and  $49\text{--}85 \mu$  diam, to occasionally obovoid, ellipsoid or irregularly ellipsoid and up to  $100 \times 70 \mu$ . Spore wall  $4\text{--}8 \mu$  thick, laminate, pale yellow, a thin outer wall barely detectable. Thickening of spore wall extending into the subtending hypha and nearly occluding the opening into the spore.

DISTRIBUTION, HABITAT, AND SEASON: Known only from a single collection in the Pacific Northwest, epigeous on the soil surface of a potted *Philodendron* sp. in the Oregon State University greenhouse. Described by Thaxter (1922) from a collection from Quebec and subsequently found in Indonesia (Boedijn, 1935, as *E. tjibodensis*).

MYCORRHIZAL ASSOCIATIONS: Unknown, but presumably with *Philodendron* spp.

ETYMOLOGY: Latin, *vesiculifer* (vesicle bearing), referring to the vesicles on sporocarps.

COLLECTION EXAMINED: OREGON—*Benton Co.*: Trappe 2077 (OSC).

As Thaxter noted, the chlamydo-spores of this species closely resemble those of *G. fasciculatus*. The only significant difference between the two species is the production of thin-walled vesicles by *G. vesiculifer*. The function of these vesicles is unknown; however, they are not immature or aborted chlamydo-spores, for the vesicles differ from spores in size, shape, and position in the sporocarp as well as in wall thickness. Thaxter's (1922) illustrations of vesicles show them to be somewhat rough and irregular at their tips. Possibly this was caused by shrinkage, as the vesicles in the Oregon collection are smooth and rounded. *Glomus vesiculifer* superficially resembles *Sclerocystis dussii* (Pat.) von Höhn., but spores of the latter are regularly elongate, septate near the base, borne in a layer over a central plexus of hyphae, and separated from the superficial vesicles by a well developed peridium of interwoven hyphae.

We have not seen *E. tjibodensis* Boedijn (1935) from Java, but from the description we consider it merely a variant of *G. vesiculifer*. Apparently the only difference of significance is the bright orange-yellow content of the vesicles of *E. tjibodensis*.



25. *Glomus microcarpus* Tul. & Tul., Giorn. Bot. Ital. Pt. 1, 2: 63. 1845.

≡ *Endogone microcarpa* (Tul. & Tul.) Tul. & Tul., Fungi Hypogaei, p. 182. 1851.

≡ *Endogone neglecta* Rodway, Proc. Roy. Soc. Tasmania 1917: 107. 1918.

Chlamydospores borne free in soil in loose aggregations, in small compact clusters unenclosed in a peridium or in sporocarps with a peridium. Sporocarps up to 5 mm broad, irregularly globose, light brown. Peridium a thin layer of interwoven hyphae similar to those in gleba, spores interspersed but less abundantly than in gleba. In sporocarps, chlamydospores 35–49  $\mu$  diam, globose to subglobose; chlamydospores free in soil 25  $\times$  25–55  $\times$  32  $\mu$ , globose, subglobose, ellipsoid, obovoid or irregular. Spore wall up to 7  $\mu$  thick, laminate, hyaline to light yellow, smooth or appearing roughened from adherent debris. Opening into subtending hypha nearly occluded in mature spores by wall thickening.

DISTRIBUTION, HABITAT, AND SEASON: Widely distributed but rather uncommon, in fields, orchards, and forests: along the coast, in the Willamette Valley, Coast Range, near timberline in the Cascade Range and east into Idaho; also reported from California (Thaxter, 1922). Hypogeous, collected in the field May to November. Ectocarpic spores probably present throughout the year. Spores develop abundantly in pot culture in 4 to 6 months. Also found in Michigan by K. Kessler and R. Blank (Trappe 3171, 3173 OSC), reported from Europe (e.g., Zycha et al., 1969), and represented in the Rodway collections from Tasmania.

MYCORRHIZAL ASSOCIATIONS: Forming vesicular-arbuscular mycorrhizae in pot culture with *Fragaria* spp., *Geum* sp., *Phleum pratense*, *Rubus spectabilis* Pursh, *Taxus brevifolia* Nutt., *Thuja plicata*, and *Zea mays* inoculated with roots of *Juniperus communis* var. *sibirica* Ait.

ETYMOLOGY: Greek, *microcarpus* (small fruited).

COLLECTIONS EXAMINED: IDAHO—*Bonner Co.*: Trappe 3059 (OSC). *Boundary Co.*: Trappe 3052, 3063 (OSC). OREGON—*Baker Co.*: leg. Iwan Ho, Trappe 3255 (OSC). *Benton Co.*: Doty 628 (NY, OSC); Trappe 2111 (OSC). *Deschutes Co.*: Trappe 2114 (OSC). *Jefferson Co.*: Trappe 2583 (OSC). *Lane Co.*: leg. Iwan Ho, Trappe 2817 (OSC). *Linn Co.*: Trappe 2115 (OSC). *Umatilla Co.*: Trappe 3050 (OSC). *Wallowa Co.*: leg. Iwan Ho, Trappe 3060 (OSC). WASHINGTON—*Chelan Co.*: leg. W. Fisher and C. Stevens, Trappe 3076 (OSC).

Sporocarps have not formed in pot cultures. Godfrey (1957a) found both sporocarps and ectocarpic spores in field collections. The type of Rodway's *Endogone neglecta* (HO) proved to be typical *Glomus microcarpus*. The isotype at FH has not been examined.

26. *Glomus fasciculatus* (Thaxter sensu Gerdemann) Gerdemann & Trappe, comb. nov.

=*Endogone macrocarpa* f. *media* Tul. & Tul., Fungi Hypogaei, p. 182. 1851.

=*Endogone fasciculata* Thaxter, Proc. Am. Acad. Arts Sci. 57: 308-309. 1922. Emend. Gerdemann, Mycologia 57: 562-575. 1965.

=*Endogone arenacea* Thaxter, Proc. Am. Acad. Arts Sci. 57: 317. 1922.

=*Rhizophagites butleri* Rosend., Bull. Torrey Bot. Club 70: 131. 1943.

Chlamydospores borne free in soil, in dead rootlets, in loose aggregations, in small compact clusters, and in sporocarps. Sporocarps up to  $8 \times 5 \times 5$  mm, irregularly globose or flattened, tuberculate, grayish brown. Peridium absent. Chlamydospores  $35-105 \mu$  diam when globose,  $75-150 \times 35-100 \mu$  when subglobose to obovate, ellipsoid, sub-lenticular, cylindrical, or irregular; smooth or seeming roughened from adherent debris. Spore walls highly variable in thickness ( $3-17 \mu$ ), hyaline to light yellow or yellow brown, the thicker walls often minutely perforate with thickened inward projections. Hyphal attachments  $4-15 \mu$  diam, occluded at maturity. Walls of attached hyphae often thickened to  $1-4 \mu$  near the spore.

DISTRIBUTION, HABITAT, AND SEASON: Widely distributed from California to British Columbia from the coast to near timberline and across the Cascade Mountains into Idaho in dunes, cultivated fields, meadows, orchards, and forests; also frequent in the greenhouse of Oregon State University. Hypogeous or, in the greenhouse, sometimes epigeous. Collected in the field most commonly in November through February. Developing abundantly in pot culture in  $3\frac{1}{2}$  to 7 months. Also reported as widely distributed elsewhere in North America and Europe (Gerdemann, 1965), and known from Trinidad (as *Endogone arenacea* Thaxter) and Australia (collection examined by Trappe from the Lloyd Herbarium, BPI).

MYCORRHIZAL ASSOCIATIONS: A common mycorrhizal fungus, probably associated with most or all endomycorrhizal hosts where it occurs; in the Pacific Northwest, found to date associated in the field with endomycorrhizae of *Chamaecyparis nootkatensis*, *Libocedrus decurrens* Torr., *Sequoia gigantea* (Lindl.) Decne., *Thuja plicata*, *Malus* spp., *Prunus* spp., *Avena sativa* L., *Lolium* sp., *Medicago sativa* L., and *Trifolium* spp.; in the greenhouse, with *Chamaecyparis lawsoniana* and *Philodendron* spp. Forming vesicular-arbuscular endomycorrhizae in pot culture with *Allium cepa*, *Clintonia uniflora* (Schult.) Kunth, *Crataegus douglasii* Lindl., *Deschampsia danthiodes* (Trin.) Munro ex Benth., *Epi-lobium watsonii* Barbey, *Fragaria vesca*, *F. chiloensis*, *Geum* sp.,

*Hypochaeris radicata*, *Maianthemum dilatatum*, *Malus* sp., *Mentha arvensis* L., *Plantago lanceolata* L., *Potentilla* sp., *Rubus spectabilis*, *R. ursinus* Cham. & Schlect., *Sitanion hystrix* (Nutt.) J. G. Smith, *Stachys mexicana* Benth., *Taxus brevifolia*, *Thuja plicata*, and *Zea mays*. Roots infected with *G. fasciculatus* sometimes become disrupted by profuse vesicle formation. Vesicles in senescent roots often become thick-walled and converted to chlamydo-spores.

ETYMOLOGY: Latin, *fasciculatus* (clustered), apparently referring to the formation of "chlamydo-spores in rounded or somewhat elongate or irregular coherent groups" (Thaxter, 1922, p. 308).

COLLECTIONS EXAMINED: BRITISH COLUMBIA—*Okanogan Valley*: Trappe 3065 (OSC). CALIFORNIA—*San Francisco Co.*: N. L. Gardner 41 (UC 296258); N. L. Gardner 144 (UC 372342). *Santa Cruz Co.*: leg. A. E. Gilmore, Trappe 2174 (OSC). *Yolo Co.*: A. E. Gilmore E-6 (OSC); leg. A. E. Gilmore, Trappe 2172, 2235 (OSC). IDAHO—*Bonner Co.*: Trappe 3055 (OSC). *Boundary Co.*: leg. Iwan Ho, Trappe 3051, 3062 (OSC). OREGON—*Benton Co.*: Trappe 2066, 2067, 2093, 2201, 2202, 2877 (OSC); leg. Iwan Ho, Trappe 2532, 2533, 2860, 2878 (OSC). *Clackamas Co.*: Trappe 2572 (OSC). *Coos Co.*: leg. Iwan Ho, Trappe 2606 (OSC). *Curry Co.*: leg. Iwan Ho, Trappe 2559 (OSC); Trappe 2787 (OSC). *Jefferson Co.*: leg. Iwan Ho, Trappe 2581 (OSC). *Lane Co.*: leg. Iwan Ho, Trappe 2587, 2749, 2757, 2818, 2843, 2880 (OSC). *Lincoln Co.*: Trappe 2200, 2223, 2226, 2229 (OSC); leg. Iwan Ho, Trappe 2836, 2870, 2873 (OSC). *Linn Co.*: leg. Iwan Ho, Trappe 2540, 2569, 2571, 2584 (OSC). *Marion Co.*: Trappe 2871 (OSC). *Tillamook Co.*: leg. Iwan Ho, Trappe 2733, 2750, 2875, 2882, 2883 (OSC). *Umatilla Co.*: leg. Iwan Ho, Trappe 3053 (OSC). WASHINGTON—*Chelan Co.*: Trappe 2844, 3057 (OSC). *Clallam Co.*: Olympic National Park, Trappe 2582 (OSC). *Okanogan Co.*: Trappe 3056 (OSC). *San Juan Co.*: leg. Iwan Ho, Trappe 3151 (OSC). *Spokane Co.*: Trappe 3054 (OSC).

Although the sporocarps in the type collections of *G. fasciculatus* and *E. arenacea* are distinctly different, the spores in the two collections do not differ in any significant respect. The type of *G. fasciculatus* was found on sphagnum, while that of *E. arenacea* (FH 5043 examined by Gerdemann) was collected from sand and consists of a mass of sand through which the spores are distributed. Differences in morphology of the sporocarps can therefore be attributed to differences in habitat.

In the size of its spores *G. fasciculatus* bridges the gap between *G. microcarpus* and *G. macrocarpus*. Possibly if enough specimens were examined, they could be arranged in a continuous series from the smallest-spored *G. microcarpus* to the largest-spored *G. macrocarpus*. Yet, combining the three species would result in an extremely great range in variability. Classification is perhaps best served at present by

retaining the three names. However, a more intensive study of the relationships within this group is needed.

If sporocarps of *G. radiatus* are sectioned across rather than along the radial alignment of chlamydospores, the spores in cross section will appear globose and their size range will overlap that of *G. fasciculatus*. However, the chlamydospores of *G. fasciculatus* are tightly packed together, while those of *G. radiatus* are grouped or widely dispersed in a matrix of coarse, thin-walled hyphae. Also, the spores of *G. radiatus* are generally filled with hyphae, a phenomenon which has not been observed in *G. fasciculatus*.

Collections Trappe 2223, 2226, and 2229 contain both terminal and intercalary chlamydospores. Intercalary spores are unusual in the Endogonaceae and certainly atypical of *G. fasciculatus*, but we feel that describing a new taxon is not appropriate for this variant until better information becomes available on the other variations of the species *sensu lato* as described here.

Spores and hyphae of occasional collections of *G. fasciculatus* (e.g. Trappe 2582) are encrusted with bacteria that appear as an artifact ornamentation of hyaline, rounded warts. The bacteria appear to be predominantly *Azotobacter*. Follow up studies on this interesting relationship are planned.

27. **Glomus macrocarpus** Tul. & Tul., Giorn. Bot. Ital. Pt. 1, 2: 63. 1845, var. **macrocarpus**. FIG. 18

==*Endogone macrocarpa* (Tul. & Tul.) Tul. & Tul., Fungi Hypogaei, p. 182. 1851.

==*Endogone australis* Berk. in Hook., Bot. Antarct. Voy. 3: 282. 1860.

==*Paurocotylis fulva* var. *zaelandica* Cooke, Grevillea 8: 59. 1879.

==*Endogone versiforme* Karst., Hedwigia 23: 39. 1884.

==*Endogone pampalomaniana* Bacc., N. Giorn. Bot. Ital. Pt. 2, 10: 79. 1903.

==*Endogone tenebrosa* Thaxter, Proc. Am. Acad. Arts Sci. 57: 314. 1922.

==*Endogone guttulata* Fischer, Schweiz. Z. Pilzkunde 1: 85-87. 1923.

==*Endogone nuda* Petch, Ceylon J. Sci. Sec. A. Ann. Roy. Bot. Gard. Peradeniya 9: 322. 1925.

Chlamydospores borne singly in soil, in loose aggregations, in sporocarps containing a considerable proportion of soil with lower portion of sporocarps generally containing more soil than the upper, or in sporocarps free of soil. Sporocarps up to 12 mm broad, irregularly globose to ellipsoid, hemispheric or consisting of a layer of spores partially enclosing a lump of soil, exterior often covered with soil particles.

Peridium white and cottony, collapsing when touched, often partially or completely absent. Sporocarps at times with immature white chlamydo-spores at the surface, becoming brown when handled. Chlamydo-spores 93–206(–230)  $\mu$  diam, usually globose to subglobose, occasionally ellipsoid or obovoid, smooth or seeming irregularly roughened from adherent debris. Spore wall up to 14  $\mu$  thick, light yellow-brown to brown, often becoming perforated at maturity. Spores with thick-walled subtending hyphae have a thin, outer wall. Thin outer wall not apparent on spores with thin-walled subtending hyphae.

DISTRIBUTION, HABITAT, AND SEASON: From coastal lowlands to the mountains and semi-arid zones of the Pacific Northwest; one of the more common *Glomus* spp. of forests, but also occurring in meadows, fields, orchards, and greenhouses. Hypogeous or, in the greenhouse, sometimes epigeous. Collected in the field throughout the year, but most commonly in late fall, winter, and spring. Forming spores in pot culture in 4 to 8 months. Widely distributed over much of the world.

MYCORRHIZAL ASSOCIATIONS: A common mycorrhizal fungus; to date in the Pacific Northwest, associated in the field with *Acer circinatum* Pursh, *A. macrophyllum* Pursh, *Sequoia gigantea*, *S. sempervirens* (D. Don) Endl., *Thuja plicata*, *Umbellularia californica* (Hook. & Arn.) Nutt., *Zea mays*, *Trifolium* sp., *Festuca* sp., *Dactylis glomerata*, and *Fragaria* spp.; and in the greenhouse, with *Philodendron* sp. and *Passiflora* sp. Forming vesicular-arbuscular mycorrhizae in pot culture with *Allium cepa*, *Epilobium glandulosum* Lehm., *Fragaria chiloensis*, *Galium aparine* L., *Stachys mexicana*, *Trifolium repens*, *Triticum aestivum*, and *Zea mays*.

ETYMOLOGY: Greek, *macrocarpus* (large-fruited).

COLLECTIONS EXAMINED (cited in two groups—those with spores often exceeding 150  $\mu$  diam, and those with spores ranging 50–150  $\mu$  diam, somewhat intermediate between “typical” *G. macrocarpus* and *G. fasciculatus*)—LARGE-SPORED: CALIFORNIA—*Del Norte Co.*: Trappe 1728, 2777, 2780 (OSC). *Marin Co.*: Harkness 237 (BPI, as *Endogone microcarpa*). *Mendocino Co.*: leg. Iwan Ho, Trappe 3121 (OSC). *Santa Clara Co.*: Parks 312 (NY). OREGON—*Benton Co.*: leg. Frank Smith, Trappe 1810 (OSC); leg. Iwan Ho, Trappe 2586, 2804 (OSC); Trappe 508, 2052, 2054, 2068, 2069 (OSC). *Coos Co.*: Trappe 2078, 2079 (OSC). *Curry Co.*: Trappe 2665, 2711 (OSC). *Grant Co.*: leg. Iwan Ho, Trappe 3230, 3258 (OSC). *Lane Co.*: leg. Iwan Ho, Trappe 2580 (OSC). *Lincoln Co.*: Trappe 603 (OSC). *Linn Co.*: Roaring River Fish Hatchery, 30 April 1938, leg. S. M. Zeller (NY). *Wheeler Co.*: leg. Iwan Ho, Trappe 3263 (OSC). *Yamhill Co.*: Gilkey 352 (OSC).

SMALL-SPORED: BRITISH COLUMBIA—*Port Mellon*: Trappe 3058 (OSC). CALIFORNIA—*Yolo Co.*: A. E. Gilmore E-3 (OSC). OREGON—*Benton Co.*: Trappe 2074, 2133 (OSC). *Coos*

Co.: Trappe 2083 (OSC). *Lane Co.*: leg. Iwan Ho, Trappe 2755, 2879 (OSC). *Lincoln Co.*: Trappe 2207 (OSC). *Linn Co.*: Trappe 2074, 2112, 2116 (OSC). *Yamhill Co.*: leg. L. T. Prier, Trappe 3231 (OSC). WASHINGTON—*Chelan Co.*: leg. W. Fisher & C. Stevens, Trappe 2919 (OSC).

We have not examined the type of *Endogone pampaloniensis*, but nothing in Baccarini's description suggests anything other than *Glomus macrocarpus*. Thaxter (1922) drew the same conclusion from examination of a fragment from the type. We have examined types of the other synonyms, and all were clearly *G. macrocarpus*. The holotype and isotype of *E. versiformis* (H) both contained sporocarps and mature chlamydospores (94–173  $\mu$  diam) typical for *G. macrocarpus*. Karsten (1884), however, gave the size of "sporangia" (chlamydospores) as 65–95  $\mu$ . A few small clusters of immature spores in this size range were found in with the soil particles associated with the sporocarps. Since these spores are immature it is not possible to know if they represent *G. macrocarpus* or *G. fasciculatus*.

28. *Glomus macrocarpus* var. *geosporus* (Nicol. & Gerd.) Gerdemann & Trappe, comb. nov.

≡ *Endogone macrocarpa* var. *geospora* Nicol. & Gerd., *Mycologia* 60: 318–319. 1968.

Chlamydospores formed singly in soil, globose to broadly ellipsoid, 110–290  $\times$  100–290  $\mu$ , smooth and shiny or roughened from adherent debris, dark brown to black. Spore wall 4–18  $\mu$  thick, dark brown to brownish black, often becoming perforated at maturity. Spores with one hyphal attachment (or rarely 2 adjacent attachments) 10–24  $\mu$  diam, the subtending hyphae with yellow to dark brown wall thickening that extends 50–150  $\mu$  along the hypha from the spore and is often perforated at maturity.

DISTRIBUTION, HABITAT, AND SEASON: Ranging from California to northern Washington. Also found in Michigan by K. Kessler and R. Blank (Trappe 3174 OSC) and Scotland (Nicolson and Gerdemann, 1968). Field collections made from May through December. Probably present in soil throughout the year.

MYCORRHIZAL ASSOCIATIONS: Associated in the field with *Avena* sp., *Bellis perennis*, *Hypochaeris radicata*, *Lolium* sp., *Malus* sp., *Prunus* sp. and *Trifolium* sp.; produced in pot culture with *Lycopersicon esculentum*, *Zea mays*, and *Fragaria* sp.

ETYMOLOGY: Greek, *geo-* (earth) and *-sporus* (spore), referring to the bearing of spores ectocarpaceally in soil and apparent absence of sporocarp formation.

COLLECTIONS EXAMINED: CALIFORNIA—*Yolo Co.*: leg. A. E. Gilmore, Trappe 2173 (OSC). OREGON—*Baker Co.*: leg. Iwan Ho,

Trappe 3254 (OSC). *Benton Co.*: leg. Iwan Ho, Trappe 2731 (OSC). *Curry Co.*: leg. Iwan Ho, Trappe 2558, 2565, 2566 (OSC). *Grant Co.*: leg. Iwan Ho, Trappe 3227 (OSC). *Marion Co.*: Trappe 2872 (OSC). *Umatilla Co.*: leg. Iwan Ho, Trappe 3251 (OSC). WASHINGTON—*Chelan Co.*: leg. E. Stahly, Trappe 2423, leg. W. Fisher and C. Stevens, Trappe 2918 (OSC). *King Co.*: leg. Iwan Ho, Trappe 3139 (OSC).

This variety is distinguished from the typical variety of *G. macrocarpus* in not forming sporocarps, in its very dark spore walls, and in the long extension of wall thickening along the spore-bearing hyphae. The last mentioned characteristic is particularly distinctive on very mature material: under low magnification, the spores appear to have long, stiff, dark brown stalks, a feature not nearly so prominent on *G. macrocarpus* var. *macrocarpus*. Young spores of var. *geosporus* are relatively light colored; however, mature spores become black and are easily distinguished from ectocarpic spores of var. *macrocarpus*. Also, when sieved from soil, the spores of var. *macrocarpus* tend to be associated in grape-like clusters whereas those of var. *geosporus* occur singly.

Very old and apparently senescent spores of var. *geosporus* frequently fill with hyaline, globose to ellipsoid, sporangiospore-like cells. This feature was omitted from the description because we are uncertain whether these cells are those of a hyperparasite or whether they are actually formed by the *Glomus* itself. If the latter case proves true, the case for a close relationship between *Glomus* and *Modicella* is greatly strengthened.

29. *Glomus caledonius* (Nicol. & Gerd.) Trappe & Gerdemann, comb. nov.

≡ *Endogone macrocarpa* var. *caledonia* Nicol. & Gerd., Mycologia 60: 318. 1968.

Chlamydospores formed singly in soil or in sporocarps. Sporocarps up to 6 mm diam, compact, subglobose, with a pallid peridium of hyaline thin-walled hyphae 8–25  $\mu$  diam and a light brown gleba. Spores dull yellow to brown, generally globose to subglobose but sometimes ellipsoid or irregular, 130–279  $\times$  120–272  $\mu$ . Spore wall 6–10(–16)  $\mu$  thick, composed of a hyaline outer layer 1–4(–8)  $\mu$  thick and a yellow to brown inner layer 4–8(–10)  $\mu$  thick; outer layer easily separable, often thickened at the hyphal attachment, and extending along the attached hypha for some distance; inner wall thickening extending into the attached hypha a short distance. Spore contents separated from attached hypha by a thin, yellow, curved wall formed at the hyphal attachment or occasionally as much as 15  $\mu$  down the attached hypha from the point of attachment.

DISTRIBUTION, HABITAT, AND SEASON: California to Washington, in fields, parks, orchards, and forests. Collected in June, September, and

December. Probably occurring in soil throughout the year. Sporulating in pot culture in 4 months.

MYCORRHIZAL ASSOCIATIONS: Associated in the field with roots of *Ginkgo biloba* L., *Trifolium repens*, and *Triticum aestivum*; forming vesicular-arbuscular endomycorrhizae with *Zea mays* in pot culture inoculated with *Triticum* roots.

ETYMOLOGY: Latin, *caledonius* (pertaining to Scotland), referring to the origin of the type collection.

COLLECTIONS EXAMINED: CALIFORNIA—*Yolo Co.*: leg. A. E. Gilmore, Trappe 3162 (OSC). OREGON—*Benton Co.*: leg. Iwan Ho, Trappe 2231, 2535 (OSC). *Marion Co.*: leg. C. Maser, Trappe 2743 (OSC). WASHINGTON—*Chelan Co.*: leg. E. Stahly, Trappe 2424 (OSC).

*Glomus caledonius* is distinctive in having thick, separable, hyaline outer spore walls. *Glomus mosseae* has a thin, hyaline outer wall that is not readily separable and additionally has a funnel-shaped hyphal attachment. Since *G. caledonius* differs more radically from *G. macrocarpus* var. *macrocarpus* than does *G. macrocarpus* var. *geosporus* or, for that matter, *G. fasciculatus*, it seems appropriate to raise *G. caledonius* from varietal to species status.

Only one sporocarp of *G. caledonius* has been found (Trappe 2743). It was growing in rotten wood supporting herbaceous plants in a young coniferous forest.

**30. *Glomus pubescens* (Sacc. & Ellis) Trappe & Gerdemann, comb. nov.**

- ≡ *Sphaerocreas pubescens* Sacc. & Ellis, *Michelia* 8: 582. 1882.
- ≡ *Stigmatella pubescens* (Sacc. & Ellis) Sacc., *Syll., Fung.* 4: 680. 1886.
- ≡ *Sclerocystis pubescens* (Sacc. & Ellis) von Höhn., *Sitzungsber. Kaiserl. Akad. Wiss. Wien Math.—Naturwiss. Kl. Abt. I.* 119: 399. 1910.
- ≡ *Endogone pubescens* (Sacc. & Ellis) Zycha, *Kryptogamenflora Mark Brandenburg* 6: 214. 1935.

Sporocarps growing on rotten sticks, globose, 0.6–1.0 mm diam, white to light brownish yellow. Peridium thin but covering most spores, composed of a tangled layer of hyaline, thin-walled hyphae 1–2  $\mu$  diam from which hyphal tips emerge both singly and in tapered fascicles to form a coarse, sparse to crowded pubescence 50–100  $\mu$  tall. Gleba yellowish brown with a basal pad of white hyphae similar to those of the peridium, the spores sometimes obscurely radially aligned from the base but more often appearing to be randomly massed. Chlamydo spores 20–48  $\times$  18–45  $\mu$ , subglobose to ellipsoid, smooth, filled with oil globules of variable size. Spore walls 3–6  $\mu$  thick, nearly hyaline to light yellow, the open-



ing occluded at maturity by wall thickening. Hyphal attachments  $\pm 2 \mu$  diam, the attached hyphae hyaline, thin-walled, and very inconspicuous.

**DISTRIBUTION, HABITAT, AND SEASON:** Known in the Pacific Northwest from only two collections from near the Oregon coast on rotten hardwood sticks (*Salix* and *Lithocarpus* spp.) in May and June. It is probably more common than this but is difficult to find because of its small size.

**MYCORRHIZAL ASSOCIATIONS:** Apparently nonmycorrhizal, either a saprophyte or hyperparasite.

**ETYMOLOGY:** Latin, *pubescens* (pubescent), referring to the peridium.

**COLLECTIONS EXAMINED:** OREGON—*Coos Co.*: Trappe 2713 (OSC). *Douglas Co.*: Trappe 2786 (OSC).

Thaxter (1922) described the spores of *G. (Sphaerocreas) pubescens* as not exceeding  $25 \times 22 \mu$ . However, our examination of Thaxter 4068 (NY) revealed many spores up to  $38 \mu$  long and one  $55 \mu$ . Numerous other collections from the Northeast (e.g. Rogerson 70-61, NY), similarly had spores commonly exceeding  $30 \mu$  in length. Spores of the Oregon collections appear to average somewhat larger than those of the Northeastern material, but the size range is similar for all.

#### EXTRALIMITAL SPECIES

**31. *Glomus fuegianus* (Spegazzini) Trappe & Gerdemann, comb. nov.**

≡ *Endogone fuegiana* Spegazzini, An. Soc. Cient. Argentina 24: 125-126. 1887.

See Thaxter (1922) and Godfrey (1957a) for descriptions of this species, which differs from other *Glomus* species in having chlamydospores that bud in groups from a thick-walled, inflated hyphal end cell. Originally described from southern South America, it has since been found in England (Godfrey, 1957a).

**32. *Glomus flavisporus* (M. Lange & Lund) Trappe & Gerdemann, comb. nov.**

≡ *Endogone flavispora* M. Lange & Lund, Friesia 5: 92-93. 1955.

Known only from the type collection from Denmark (C), this species has the largest spores ( $149-230 \times 95-152 \mu$ ) of the ellipsoid-spored *Glomus* spp. Spore walls are brown,  $10-13 \mu$  thick, continuous except for the attachment, which is closed by a thin septum.

**33. *Glomus borealis* (Thaxter) Trappe & Gerdemann, comb. nov.**

≡ *Endogone borealis* Thaxter, Proc. Am. Acad. Arts Sci. 57: 318. 1922.

This species, known only from the type collection from Quebec (FH), differs from *G. flavisporus* in having smaller spores ( $125\text{--}145 \times 100\text{--}110 \mu$ ). Its spore walls are darker and thicker than the walls of *Glomus* species with still smaller, ellipsoid spores.

34. *Glomus canadensis* (Thaxter) Trappe & Gerdemann, comb. nov.

≡*Endogone canadensis* Thaxter, Proc. Am. Acad. Arts Sci. **57**: 317–318. 1922.

This species is known only from collections (FH 5045, type and 5046) from Quebec. It is characterized by ovoid to ellipsoid spores not greater than  $100 \mu$  in length. There is a septum at the spore base and the spore wall thickening does not extend into the sporophore.

35. *Glomus fulvus* (Berk. & Broome) Trappe & Gerdemann, comb. nov.

≡*Paurocotylis fulva* Berk. & Broome, J. Linn. Soc. London (Bot.) **14**: 137. 1875.

≡*Endogone fulva* (Berk. & Broome) Pat., Bull. Soc. Mycol. France **19**: 341. 1903.

≡*Endogone moelleri* Hennings, Hedwigia **36**: 211. 1897.

≡*Endogone lignicola* Pat., Bull. Soc. Mycol. France **18**: 183. 1902.

See Thaxter (1922) for a detailed description of this species, which is relatively common in tropical America and also occurs in Ceylon and the South Pacific area (e.g., Zycha et al., 1969). Aside from its apparent restriction to the tropics, it differs from *G. canadensis* in having larger sporocarps, spores that range somewhat larger ( $70\text{--}120\text{--}160 \times 50\text{--}80 \mu$  vs.  $70\text{--}100 \times 54\text{--}70 \mu$ ), and a broader hyphal attachment ( $8\text{--}15 \mu$  vs.  $4\text{--}5 \mu$ ).

36. *Glomus pulvinatus* (Hennings) Trappe & Gerdemann, comb. nov.

≡*Endogone pulvinata* Hennings, Hedwigia **36**: 212. 1897.

This species differs from *G. fulvus* primarily in having globose to subglobose spores,  $65\text{--}82\text{--}100 \times 65\text{--}90\text{--}105 \mu$ , and from *G. fragilis* (Berk. & Broome) Trappe & Gerd. in having single walled, larger spores with broader hyphal attachments. It has been found only in tropical America and Tasmania (Thaxter, 1922), and New Zealand (PDD 29715).

37. *Glomus fragilis* (Berk. & Broome) Trappe & Gerdemann, comb. nov.

≡*Paurocotylis fragilis* Berk. & Broome, J. Linn. Soc. London **14**: 137. 1875.

The globose to subglobose spores of *G. fragilis*, as determined from the type (K, Berkeley 1182) are  $53-73 \times 49-62 \mu$  and have attachments  $6-9(-13) \mu$  broad. The spore is separated from attached hyphae by a septum. It has smaller spores and hyphal attachments than *G. pulvinatus*, but additionally differs from that species in having a distinctly 2-layered spore wall. The outer wall is hyaline and  $0.5-0.7 \mu$  thick, and the inner wall is pale yellow and  $2-2.5 \mu$  thick. *Glomus fragilis* is known only from the type collection from Ceylon.

**V. SCLEROCYSTIS** Berk. & Broome, J. Linn. Soc. London **14**: 137. 1875.

*Type species: Sclerocystis coremioides* Berk. & Broome.

*Xenomycetes* Cesati, Atti R. Accad. Sci. Fische e Math. Napoli **8** (No. 4): 26. 1879.

*Ackermannia* Patouillard, Bul. Soc. Mycol. France **18**: 180. 1902.

Chlamydospores arranged side by side in a single layer, elongate, radiating out from a central plexus of hyphae.

ETYMOLOGY: Greek, *sclero-* (hard) and *-kystis* (bladder), referring to the small, very hard, rounded sporocarps of the type species.

As a chlamydosporic genus, *Sclerocystis* differs from *Glomus* only in having its spores arranged in a single, orderly layer around a central, spore-free plexus. This difference may be of questionable value in separation of genera. However, it would appear to be an evolutionary advance in sporocarp morphology from *Glomus*, and synonymizing the two genera would serve no useful purpose at this time.

Two of the three species found in Oregon occurred on soil around tropical plants in a greenhouse; since they have been previously collected only in the tropics, subtropics, or a greenhouse they are not likely native to the Pacific Northwest. A third species, *S. rubiformis* Gerdemann & Trappe, is widely distributed in Oregon and is presumably native. Probably all *Sclerocystis* species form vesicular-arbuscular mycorrhizae.

KEY TO THE SPECIES OF SCLEROCYSTIS

- |  |                           |
|--|---------------------------|
| 1. Sporocarps not enclosed in a peridium .....   | 38. <i>S. rubiformis</i>  |
| 1. Sporocarps enclosed in a peridium .....   | 2                         |
| 2. Sporocarps fused together in a mat that is covered with large, thin-walled vesicles ..... | 40. <i>S. dussii</i>      |
| 2. Sporocarps single or fused in a mat, but lacking a cover of vesicles .....                | 3                         |
| 3. Peridium containing scattered small, globose chlamydospores (extralimital species) .....  | 41. <i>S. coccogena</i>   |
| 3. Peridium lacking small, globose chlamydospores .....                                      | 39. <i>S. coremioides</i> |

**38. Sclerocystis rubiformis** Gerdemann & Trappe, sp. nov.

FIGS. 23-25

Sporocarpia fusco-brunnea, subglobosa vel ellipsoidea,  $180 \times 180-375 \times 675 \mu$ , e strato chlamydosporarum uno medullam e hyphis intertextam obducente con-

stantia, instar fructuum (e drupeolis et toro compositorum) ruborum nonnullorum. Peridium minimum, sporis singulis interdum in reticulo tenui e hyphis arcte appressis composito partim inclusis. Chlamydo sporae fusco-brunneae, obovoideae, ellipsoideae, vel subglobosae,  $37-125 \times 29-86 \mu$ , poro stricto in hypham crasse tunicatam sustentantem continuo. Sporae tunica laminata,  $3-7.6 \mu$  vel prope basim ad  $13.5 \mu$  crassa, maturiorae saepe perforata et e superficie interna prominentias perforatas efformans.

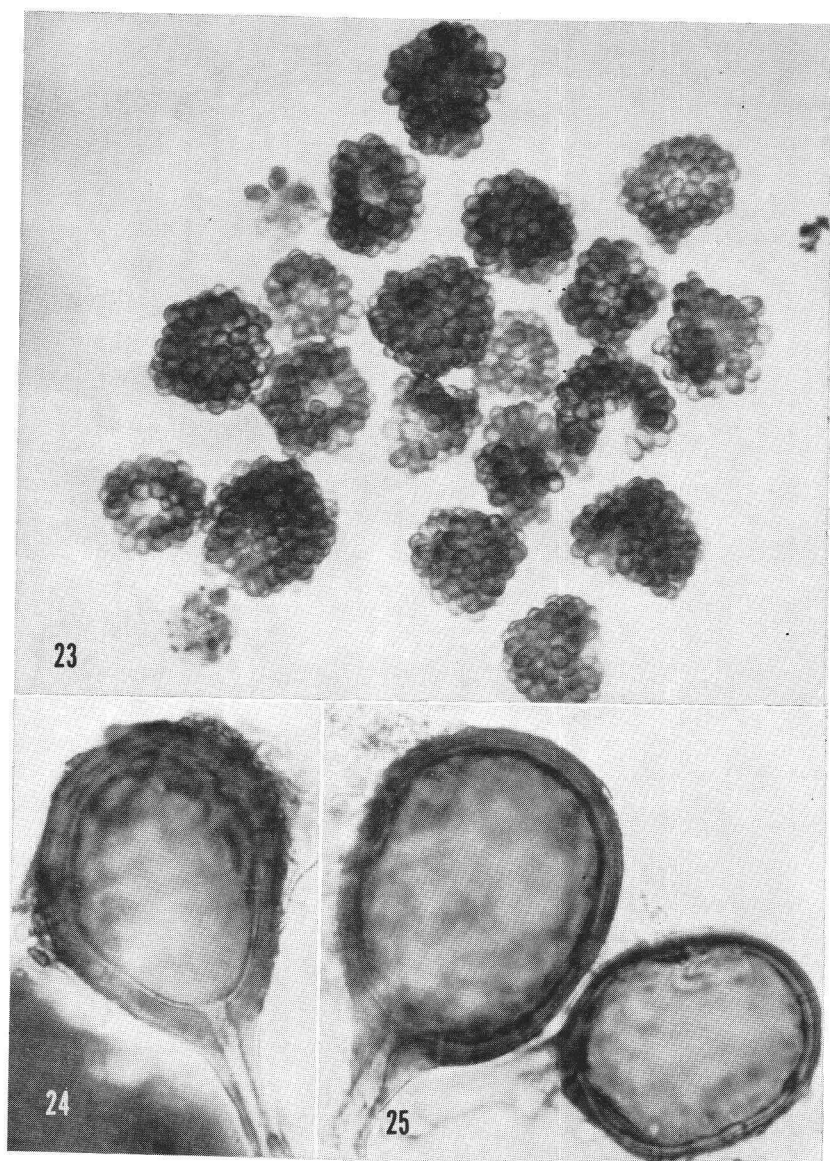
Sporocarps dark brown, subglobose to ellipsoid,  $180 \times 180-375 \times 675 \mu$ , consisting of a single layer of chlamydo spores surrounding a central plexus of hyphae, resembling a miniature blackberry. Peridium nearly absent, individual spores at times partially enclosed in a thin network of tightly appressed hyphae. Chlamydo spores dark brown, obovoid to ellipsoid or subglobose,  $37-125 \times 29-86 \mu$ , with a small pore opening into the thick-walled subtending hypha. Spore wall laminate,  $3-7.6 \mu$  thick, up to  $13.5 \mu$  thick at spore base, often perforated, and often with thick, perforated projections on the inner surface. A variable stalk-like projection protrudes near the base of some spores.

DISTRIBUTION, HABITAT, AND SEASON: Found in Oregon and Washington in fields and orchards east of the Cascade Mountains, in dry-land grain fields of Willamette Valley, under trees on the Oregon State University campus, in beach dune sands, in montane meadows in the Coast and Cascade Ranges, and in soil from a potted *Philodendron* sp. Also found in Michigan by K. Kessler and R. Blank (Trappe 3168, 3176 OSC). A similar, or perhaps identical, species, was reported by Mosse and Bowen (1968a) to occur in New Zealand, England, and Wales. Collected in the field throughout the year.

MYCORRHIZAL ASSOCIATIONS: Associated in the field with endomycorrhizae of *Chamaecyparis lawsoniana*, *Dactylis glomerata*, *Fragaria virginiana* Duch., *Hypochaeris radicata*, *Lolium multiflorum*, *Medicago sativa*, *Festuca subulata*, *Thuja plicata*, *Trifolium repens*, *Triticum aestivum*, *Zea mays*, and forming mycorrhizae and sporulating with *Zea mays* and *Lycopersicon esculentum* in pot cultures inoculated with sporocarps.

ETYMOLOGY: Latin, *rubiformis* (having the form of *Rubus*), referring to the resemblance of sporocarps to miniature *Rubus* fruit.

COLLECTIONS EXAMINED: TYPE: OREGON—*Benton Co.*: Oregon State University campus, near the southeastern corner of the Forestry Sciences Laboratory parking lot, from around roots of *Trifolium repens* and various grasses by wet-sieving and decanting, 19 August, 1969, Trappe 2108 (OSC). PARATYPES: OREGON—*Benton Co.*: Trappe 1988 (OSC); leg. Iwan Ho, Trappe 2150, 2153, 2204, 2217, 2219, 2222, 2536, 2556 (all OSC). *Coos Co.*: leg. C. Maser, Trappe 3203 (OSC). *Deschutes Co.*: leg. Iwan Ho, Trappe 3222 (OSC). *Grant Co.*: leg. Iwan Ho, Trappe 3259 (OSC). *Klamath Co.*: leg. Iwan Ho, Trappe 2874 (OSC). *Lane Co.*: leg. Iwan Ho, Trappe 2588 (OSC). WASHINGTON—*Chelan Co.*: leg. W. Fisher and C. Stevens, Trappe 2920 (OSC). *King Co.*: leg. Iwan Ho, Trappe 3141 (OSC).



FIGS. 23-25. Sporocarps and chlamydospores of *Sclerocystis rubiformis*. 23. Sporocarps,  $\times 50$ . 24-25. Chlamydospores,  $\times 625$ .

Sporocarps of *S. rubiformis* closely resemble those formed by *S. coremioides*. They are easily distinguished by the near absence of a peridium in *S. rubiformis*.

39. **Sclerocystis coremioides** Berk. & Broome, J. Linn. Soc. London  
14: 137. 1875. FIG. 26

= *Xenomycetes ochraceus* Cesati, Atti R. Acad. Sci. Fische e Math.  
Napoli 8 (No. 4): 26. 1879.

= *Sphaerocreas javanicum* von Höhn., Sitzungsber. Kaiserl. Akad.  
Wiss. Wein Math.—Naturwiss. Kl. Abt. I. 117: 1014. 1908.

= *Endogone minutissima* Beeli, Bull. Soc. Roy. Belg. 56: 57.  
1923.

Sporocarps 340–600  $\mu$  broad, subglobose to pulvinate, flattened at base, at times borne on a short stalk up to 100  $\mu$  broad, white when immature, becoming tan to dull brown when fully mature, gregarious in mats containing large numbers of sporocarps fused together laterally and one above the other to about 4 sporocarps thick. Peridium 20–70  $\mu$  thick, of interwoven hyphae. Chlamydo-spores 50–86(–102)  $\times$  35–52(–82)  $\mu$ , obovoid-ellipsoid to oblong-ellipsoid, often but not always cut off from subtending hyphae by septa just below spore base, arranged in a single layer, tightly grouped in a hemisphere around a central plexus of hyphae. Spores absent at base of sporocarp. Chlamydo-spore wall up to 4  $\mu$  thick at base and 2  $\mu$  thick at apex, brown. Forming vesicular-arbuscular mycorrhizae.

DISTRIBUTION, HABITAT, AND SEASON: Known in the Pacific Northwest only from the botany greenhouse of Oregon State University at Corvallis, where it fruits abundantly on the surface of soil and organic matter of pots of tropical and subtropical plants throughout the year. Probably introduced, having otherwise been reported only from the South Pacific tropics (e.g. Thaxter, 1922; Boedijn, 1935) and, recently, from Florida (Schenck and Hinson, 1971).

MYCORRHIZAL ASSOCIATIONS: Vesicular-arbuscular mycorrhizae formed on *Zea mays* inoculated with sporocarps collected from a potted *Musa* sp. Sporocarps also formed in pots of these presumably mycorrhizal hosts: *Aglaonema* sp., *Allamanda schottii* Pohl, *Crinum moorei* Hook., *Ficus pandurata* Hort., *Hedychium* sp., *Maranta leuconeura* Morr., *Musa* sp., *Nerium* sp., *Plectranthus* sp., *Polyscias balfouriana* Bailey, *Schefflera* sp.

ETYMOLOGY: Greek, *coremioides* (resembling a broom); Berkeley and Broome did not indicate why this name was chosen and their intent is now obscure.

COLLECTIONS EXAMINED: OREGON—*Benton Co.*: Trappe 2049, 2080, 2123, 2125, 2126, 2127, 2128, 2130, 2131, 2135, 2136, 2137, 2138 (OSC).

*Endogone minutissima* proved, from our examination of the type

(BR, Beeli 93), to be typical *S. coremioides*. It was collected in the Botanical Garden at Brussels from organic matter. Like the Oregon collections, it was probably imported on roots of plants from the tropics.

40. *Sclerocystis dussii* (Pat.) von Höhn., Sitzungsber. Kaiserl. Akad. Wiss. Wien Math.-Naturwiss. Kl. Abt. I. 119: 399. 1910.

FIG. 27

≡ *Ackermannia dussii* Pat., Bull. Soc. Mycol. France 18: 180-181. 1902.

≡ *Sphaerocreas dussii* (Pat.) von Höhn., Sitzungsber. Kaiserl. Akad. Wiss. Wien Math.-Naturwiss. Kl. Abt. I. 118: 401. 1909.

Sporocarps 263-540  $\mu$  broad, subglobose to hemispheric, pulvinate, or pyriform, single to fused together laterally and vertically to a depth of 3 or 4, forming a tuberculate crust on soil surface; whitish when young, becoming tan by maturity or where bruised; upper surface of crust covered with thin-walled vesicles up to  $340 \times 77 \mu$ , globose when young, becoming obovoid to ellipsoid to clavate or broadly clavate and rounded at the tip, at times constricted near middle, collapsing when dried. Peridium of individual sporocarps 20-60  $\mu$  thick, composed of thick-walled interwoven hyphae. Chlamydospores 50-80  $\times$  32-54  $\mu$ , obovate to clavate, ellipsoid or oblong-ellipsoid, cut off from subtending hyphae by septa just below spore bases, tightly grouped in a single layer in a hemisphere around a central plexus of hyphae. Spores absent at sporocarp base. Chlamydospore wall up to 3  $\mu$  thick at base and 2  $\mu$  at apex, brown. Odor of fresh specimens distinctly of fish (very noticeable when kept moist in closed container).

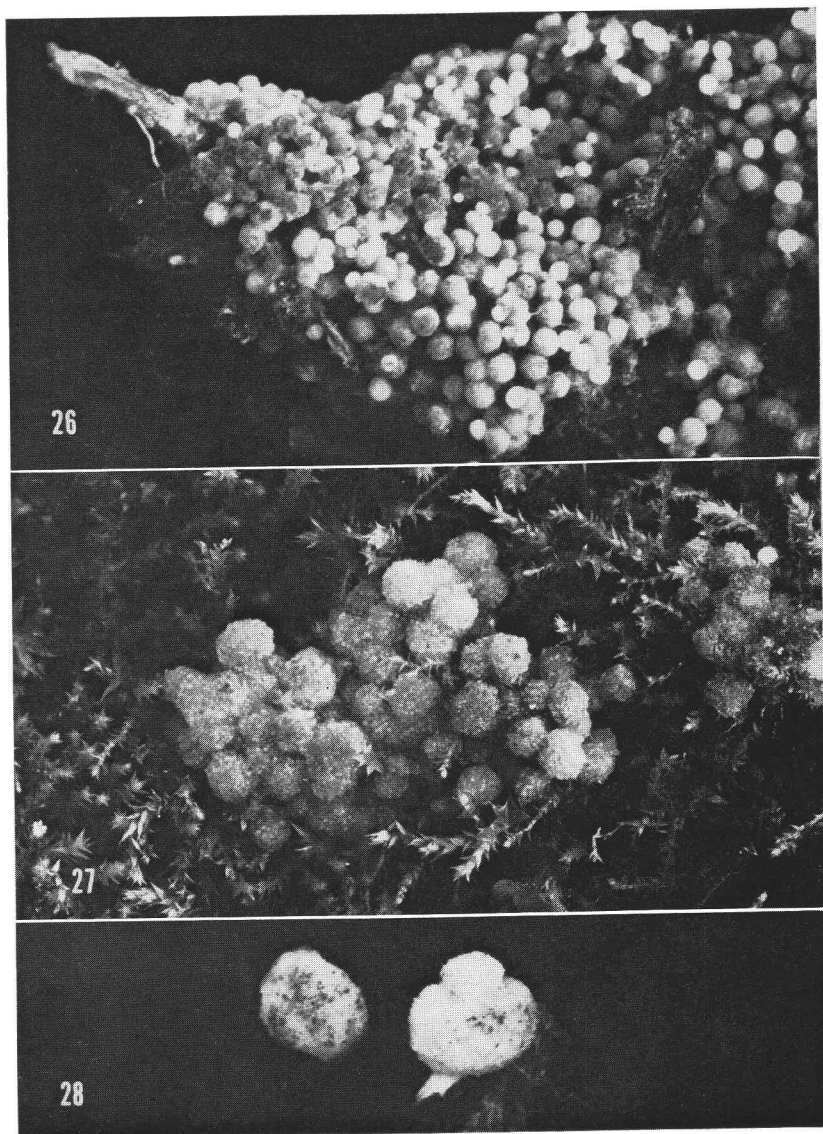
DISTRIBUTION, HABITAT, AND SEASON: Known in the Pacific Northwest only from the botany greenhouse of Oregon State University at Corvallis, where it fruits abundantly on the soil surface, often among mosses, of pots of tropical and subtropical plants throughout the year. Probably introduced, having otherwise been reported only from the Caribbean area [Thaxter, 1922; Martin, 1939, as *Sclerocystis coccogena* (Pat.) von Höhn.].

MYCORRHIZAL ASSOCIATIONS: Fruiting on soil of pots of these presumed mycorrhizal hosts: *Heliconia bihai* Linn., *Hibiscus rosa-sinensis* Linn., *Philodendron* sp., *Plectranthus* sp., and *Schefflera* spp.

ETYMOLOGY: Named in honor of R. P. Duss, the collector of the type.

COLLECTIONS EXAMINED: OREGON—*Benton Co.*: Trappe 2084, 2119, 2122, 2129, 2132, 2134, 2139 (OSC).

The Oregon collections of *S. dussii* are identical to Duss's collection 211 and 616 in the Patouillard Herbarium (FH). Thaxter (1922) expressed doubt that the species was distinct from *S. coremioides*, largely on the basis that he could not observe large vesicles on the surface of sporocarps as described by Patouillard. Indeed, Thaxter's illustrations



FIGS. 26-28. Sporocarps of *Sclerocystis* and *Modicella*. 26. *Sclerocystis coremioides*,  $\times 6.8$ . 27. *Sclerocystis dussii*,  $\times$  ca. 16. 28. Sporocarps of *Modicella malleola*, view of upper-surface,  $\times 6.6$ .



do not accurately portray the vesicles. The vesicles collapse upon drying, and if such material is sectioned somewhat obliquely and mounted in water or lactophenol, it can closely resemble Thaxter's illustration. If well preserved, dried material is mounted in 5% KOH, however, the vesicles tend to revive to their normal shape. Our examination of fresh specimens fully confirms Patouillard's description. Confusion can arise in that many or most of the large vesicles of *S. dussii* sometimes disappear. In the case of Trappe 2119, this apparently resulted from feeding by free-living nematodes that were abundant in the freshly collected material.

The vesicles of *S. dussii* remarkably resemble those of *Glomus vesiculifer*. In their respective genera, both species have counterparts which they resemble very closely and which differ from them primarily in lacking vesicles. Without vesicles *G. vesiculifer* would probably not be distinguishable from *G. fasciculatus*, and when vesicles are removed from *S. dussii*, it closely resembles *S. coremioides*. The question must be raised whether such vesicles are simply a rare stage in the life cycle of two species. On the basis of observations in the Oregon State University greenhouse, *S. coremioides* and *S. dussii* appear to be distinct: they were seldom found fruiting together in the same pot, but when this occurred the colonies were distinctly separated.

#### EXTRALIMITAL SPECIES

41. ***Sclerocystis coccogena*** (Pat.) von Höhn., Sitzungsber. Kaiserl. Akad. Wiss. Wien Math.-Naturwiss. Kl. Abt. I. 119: 399. 1910.  
 ≡ *Ackermannia coccogena* Pat., Bull. Soc. Mycol. France 18: 183. 1902.  
 ≡ *Sphaerocreas coccogena* (Pat.) von Höhn., Sitzungsber. Kaiserl. Akad. Wiss. Wien Math.-Naturwiss. Kl. Abt. I. 118: 401. 1909.

See Thaxter (1922) for a description of this species, known only from the type collection from the Caribbean Island of Martinique. It differs from other *Sclerocystis* spp. in having small, globose chlamydo-spores scattered in and on the peridium. Martin (1939) also reported *S. coccogena* from Columbia (Martin 3609—BPI, FH, and NY); our examination of this collection showed it to be *S. dussii*.

#### VI. **MODICELLA** Kanouse, Mycologia 28: 60. 1936.

*Type species: Endogone malleola* Harkn.  
*Endogone* p. p.

Sporocarps epigeous or hypogeous, firm, consisting only of sporangia and hyphae. Sporangia terminal on hyphae, thin-walled, hyaline, lacking a columella. Sporangiospores smooth, hyaline, ellipsoid.

ETYMOLOGY: Latin, *modicellus* (small size), referring to the small sporocarps of the type species.

Kanouse (1936) described the genus *Modicella* for the sporangial *Endogone* species and *E. malleola* was designated as the type; however, the formal transfer of species into the new genus was not made. *Modicella* species produce sporangia in small compact epigeous sporocarps. No other type of fruiting has been observed. The sporangia lack columellae, suggesting a relationship with the Mortierellaceae (Thaxter, 1922; Walker, 1923), and Kanouse tentatively placed *Modicella* in the Mortierellaceae. We have followed Thaxter in retaining the sporangial species within the Endogonaceae but without any great conviction that they are closely related to the other species. Until more information is available, we believe little is gained by transferring sporangial species from the family. At the same time, we also question the supposition that the sporangial species necessarily provide evidence for a relationship of other Endogonaceae to the Mortierellaceae.

Walker (1923) obtained *M. malleola* in pure culture but was unable to obtain any kind of fruiting. Masses of moniliform cells somewhat resembling sporocarps were produced on agar media but sporangia never developed within them. There is no evidence whether *Modicella* species form mycorrhizae.

#### KEY TO THE SPECIES OF MODICELLA

1. Sporangia 55–118  $\times$  50–91  $\mu$ ; spores 7–17  $\mu$  long ..... 42. *M. malleola*  
 1. Sporangia rarely exceeding 60  $\mu$ ; spores 12–30(–38)  $\mu$  long (extralimital species) ..... 43. *M. reniformis*

#### 42. *Modicella malleola* (Harkn.) Gerdemann & Trappe, comb. nov.

FIG. 28

=*Endogone malleola* Harkn., Proc. Cal. Acad. Sci. Ser. 3, 1: 280. 1899.

=*Endogone torrendii* Bres. in Torrend, Broteria 11: 101. 1913.

Sporocarps 2–5 mm broad, globose to subglobose or pulvinate, smooth to slightly lobed, indented at base, hard; white, drying to pale, dirty yellow. Peridium absent. Lower portion of sporocarp consisting of hyphae which radiate from the base; upper portion, of sporangia. Sporangia 55–118  $\times$  50–91  $\mu$ , globose to subglobose, ellipsoid, or irregular, hyaline, thin-walled, terminal on hyphae 8–12  $\mu$  diam, compressed tightly together. Spores 7–17  $\mu$  long, subglobose to ellipsoid but distinctly subangular from mutual pressure, hyaline, thin-walled, coherent in clusters when forced out of sporangia. Odor of fresh specimens distinctly of onions (perceptible when kept moist for awhile in a closed container).

DISTRIBUTION, HABITAT, AND SEASON: KNOWN from northwestern

Washington, the Willamette Valley and coast of Oregon, and coastal California in stands of *Quercus*, *Pseudotsuga*, *Sequoia*, or mixed forests. Epigeous on bark or among mosses or hypogeous under moss or litter; mostly collected in April and May, but also found in November. Also reported from Nebraska (Walker, 1923), Europe and New Zealand (Thaxter, 1922).

MYCORRHIZAL ASSOCIATIONS: Unknown, but often fruiting in the complete absence of endomycorrhizal hosts.

ETYMOLOGY: Latin, *malleolus* (a small mallet); Harkness's intent in use of this epithet is unknown, but it possibly refers to the sporangia with attached hyphae, which in his illustration could be thought to appear mallet-like.

COLLECTIONS EXAMINED: CALIFORNIA—*Marin Co.*: N. L. Gardner 169 (UC 1273111). OREGON—*Benton Co.*: Trappe 2615, 2616, 2649 (OSC). *Coos Co.*: Trappe 2708, 2709 (OSC). *Curry Co.*: Trappe 2712 (OSC). *Linn Co.*: Trappe 2605 (OSC). *Polk Co.*: Trappe 2648 (OSC). WASHINGTON—*King Co.*: Hosford 271 (CWSC, OSC).

#### EXTRALIMITAL SPECIES

#### 43. *Modicella reniformis* (Bres.) Gerdemann & Trappe, comb. nov.

≡ *Endogone reniformis* Bres., *Hedwigia* 35: 297. 1896.

= *Endogone argentina* Speg., *An. Mus. Nac. Buenos Aires* 6: 300. 1899.

See Thaxter (1922) for a description of this species, known only from South America. It differs from *M. malleola* in having smaller sporangia but larger sporangiospores.

#### VII. *GLAZIELLA* Berk., *Vidensk. Medd. Naturh. For. Kjøbenhavn* p. 31 1879/1880 (extralimital genus).

*Type species: Glaziella aurantiaca* (Berk. & Curtis) Cooke.

*Endogonella* von Höhn., *Sitzungsber. Kaiserl. Akad. Wiss. Wien Math.-Naturwiss. Kl. Abt. I.* 122: 294. 1913.

Sporocarps 1.5 to 5 cm broad, hollow. Chlamyospores scattered in the thin sporocarp walls.

ETYMOLOGY: Named in honor of Dr. A. Glaziou.

The genus is represented only in the American, South Pacific and East Indian tropics near beaches. Only one species is recognized.

#### EXTRALIMITAL SPECIES

#### 44. *Glaziella aurantiaca* (Berk. & Curtis) Cooke, *Grevillea* 11: 83. 1883.

- = *Xylaria aurantiaca* Berk. & Cutris, J. Linnean Soc. 10:382.  
 1869.  
 = *Glaziella vesiculosa* Berk., Vidensk. Medd. Naturh. For. Kjø-  
 benhavn p. 31. 1879/1880.  
 = *Endogonella borneensis* von Höhn., Sitzungsber. Kaiserl. Akad.  
 Wiss. Wein Math.-Naturwiss. Kl. Abt. I. 122:295. 1913.  
 = *Glaziella berkeleyi* Lloyd, Mycol, Notes 7:1204. 1923.

Sporocarps 1.5–5 cm broad, hollow, bright orange or scarlet when fresh, drying to pale yellow. Chlamydo-spores globose to ellipsoid up to 415  $\mu$ , scattered in the thin sporocarp walls.

For detailed descriptions and discussions of this species see Thaxter (1922), Boedijn (1930), and Rogers (1947).

### EXCLUDED SPECIES

*Endogone irregularis* Szemere, Die unterirdischen Pilze des Karpatenbeckens, Akad. Kaidó, Budapest, p. 86. 1965.

The type (BP) is essentially as originally described. The "spores" have no attachments of any kind, and no hyphae are present. It is clearly not a member of the Endogonaceae. We could not even be sure that it is of fungal origin.

The following species were excluded from the Endogonaceae by Thaxter (1922); *Endogone tozziana* Sacc. & Cav., p. 326; *Glaziella abnormis* (Berk.) Cooke, *G. ceramichroa* (Berk. & Broome) Cooke, *G. splendens* Cooke, *G. sulphurea* Pat., p. 338. The following were excluded by Boedijn (1930): *Glaziella bakeriana* Sacc., *G. cyttarioides* Speng., p. 58.

### MEANS OF DISPERSAL

Species of Endogonaceae, with the exception of *Modicella* spp., have relatively large, heavy spores and all lack a mechanism for forcible spore discharge. In addition, most species fruit hypogeously. Accordingly, they are dependent on external forces for dispersal. Two means of dispersal are certain and a third can be hypothesized. The known means of dispersal are (1) transplantation of host plants with mycorrhizal infections and (2) physical movement of spores and sporocarps with soil. The hypothetical means is by ingestion and subsequent defecation of spores by animals and insects.

As indicated in "Materials and Methods," Endogonaceae often sporulate abundantly in pots containing endomycorrhizal plants transplanted from the field. Living, mycorrhizal plants have been transported over long distances for many centuries; the mycorrhizal fungi accompany the host as "hitchhikers" in the roots. Undoubtedly this is the way in which

tropical species such as *Sclerocystis coremioides* came to greenhouses in Oregon and Belgium.

The abundance of spores and sporocarps of Endogonaceae in soil assures that all of the agents that move soil will also transport these fungi. Thus, they may be carried by strong wind or water, on the feet of animals, on the wheels of automobiles, agricultural or construction equipment, or even the shoes of man.

Movement by ingestion and defecation by animals is still hypothetical because viability of spores thus treated has not been tested. However, spores of Endogonaceae are common in stomachs of several species of small rodents (Diehl, 1939; Dowding, 1959; Whitaker, 1963; Harling and McClaren, 1970 and numerous others). Mammalogists well acquainted with the ecology of these rodents present evidence that they actively seek and feed upon spores of Endogonaceae (Whitaker, 1963; Harling and McClaren, 1970) rather than ingest them accidentally with other food as proposed earlier by some mycologists (Bakerspigel, 1958b; Dowding, 1959).

We have examined stomach contents of three species of rodents from the Pacific Northwest, as kindly provided by Mr. Chris Maser, University of Puget Sound Museum of Natural History, Tacoma, Washington, and Dr. Milton McClaren, Simon Fraser University, Burnaby, British Columbia. Most of the stomachs contained fungi, and many included spores of Endogonaceae. Contents of the latter varied from a few spores in some individuals to an estimated 80% of the total volume in one. In most cases, spores of Endogonaceae comprised an estimated 5 to 15% of the total stomach content volume.

The Endogonaceae ingested by these rodents included zygosporic and chlamydosporic species. All of the species that have been identified are known to produce sporocarps, which are probably more easily found and ingested by animals than single spores. Western red-backed mice *Clethrionomys occidentalis californicus* (Merriam) contained *Endogone flammicorona*, *E. lactiflua*, *E. pisiformis*, *Glomus fasciculatus*, *G. macrocarpus* var. *macrocarpus*, *G. microcarpus*, *G. monosporus*, and *Sclerocystis rubiformis*. Deer mice *Peromyscus maniculatus* (Wagner) had *Endogone flammicorona*, *E. lactiflua*, *E. pisiformis*, *Glomus caledonius*, *G. macrocarpus* var. *macrocarpus*, *G. microcarpus*, and *Sclerocystis rubiformis*. Pacific jumping mice *Zapus trinotatus* Rhoads contained *Endogone lactiflua*, *Glomus fasciculatus*, *G. monosporus*, and *Sclerocystis rubiformis*. Most individual animals contained at least 2 species of Endogonaceae, several had 3 or 4 species, and one deer mouse had 5. The absence of *Acaulospora* spp. and *Gigaspora* spp. from stomachs of animals may be meaningful in view of the fact they are not known to produce sporocarps.

For some of the mammals examined, feces as well as stomach contents were available. In all cases, well-matured spores appeared to have

passed through the digestive tract without morphological change. Hyphae, on the other hand, showed various stages of disintegration in stomach contents and were generally unrecognizable in feces. Strictly on a morphological basis, it appears that rodents digest mycelium of Endogonaceae but pass the spores unharmed. Hypothetically, then, animals serve as vectors for spore dispersal, but confirmation of the hypothesis requires firm evidence on the viability of the excreted spores.

Insects may serve as spore dispersers for the Endogonaceae in the same way as small mammals. Hansen and Ueckert (1970) reported ingestion of fungi by crickets and grasshoppers. Some of the fungal material was subsequently identified as spores of Endogonaceae (R. M. Hansen, personal communication).

### ACKNOWLEDGMENTS

We are indebted to the herbaria listed in the Methods Section for loan of specimens, as well as to these individuals: Professor Lilian Hawker, University of Bristol; Dr. David Hosford, Central Washington State College; and Mrs. Phyllis Kempton and Mrs. Virginia Wells of Anchorage, Alaska.

Inspection of our lists of collections examined also readily reveals the large amount of dedicated effort by Mr. Iwan Ho, U.S. Forest Service, Pacific Northwest Forest and Range Experiment Station, Forestry Sciences Laboratory, Corvallis, Oregon, in pot culturing and collecting and sieving soils. Other personnel of the laboratory contributed substantially in many ways, especially microtechnician Mrs. Darr Duff and Miss Koren Grossnicklaus, whose typing of several drafts of the manuscript have surely resulted in her being a foremost expert on the Endogonaceae. Professor D. P. Rogers, University of Illinois, kindly prepared the Latin diagnoses.

Dr. Gerdemann devoted 6 months to sabbatical research at the Forestry Sciences Laboratory. He is deeply grateful to the Pacific Northwest Forest and Range Experiment Station for the facilities and equipment provided. Dr. Trappe's participation in the research was supported in part by National Science Foundation Grant GB-27378.

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