

Lectotypification of *Glomus macrocarpum* and proposal of new combinations: *Glomus australe*, *Glomus versiforme*, and *Glomus tenebrosus* (Endogonaceae)

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A lectotype is designated for *Glomus macrocarpum* Tul. & Tul. from the original Tulasne collections. As a consequence of the examination of type materials of previously proposed synonyms of this species, three new combinations are made: *Glomus australe* (Berk.) Berch, *Glomus versiforme* (Karst.) Berch, and *Glomus tenebrosus* (Thaxter) Berch.

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Un lectotype est sélectionné pour *Glomus macrocarpum* Tul. & Tul. parmi les collections originales de Tulasne. Le matériel-type des taxons antérieurement proposés comme synonymes de cette espèce a été examiné et, à la suite de cette étude, trois nouvelles combinaisons sont effectuées: *Glomus australe* (Berk.) Berch, *Glomus versiforme* (Karst.) Berch et *Glomus tenebrosus* (Thaxter) Berch.

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Introduction

Most known species of *Glomus* Tul. & Tul. (Endogonaceae, Endogonales, Zygomycetes) have been demonstrated to form the fungus–plant symbiosis known as vesicular–arbuscular mycorrhiza (VAM). This mutualistic association, by facilitating the growth of the majority of land plants including most agricultural and horticultural and even some forestry crops, has become the focus of a great deal of scientific energy. Research towards the eventual practical applications of this symbiosis has revealed differences in efficiency among species and isolates of *Glomus* (cf. Mosse 1975). To ensure that experiments can be compared and results reproduced, it must be possible to identify these fungi with confidence.

In their monograph of the Endogonaceae, Gerdemann and Trappe (1974) pointed out a particular need for detailed study of the relationships within the *Glomus microcarpum* Tul. & Tul., *G. fasciculatum* (Thaxter) Gerd. & Trappe, and *G. macrocarpum* Tul. & Tul. group. These fungi are commonly used in VAM research and thus clarity of their taxonomy is of critical and immediate importance.

Gerdemann (1965) designated a lectotype for *Glomus fasciculatum* and then described contemporary isolates pot cultured on host plants. He did not, however, describe or illustrate the lectotype material, and Thaxter's original description is not sufficiently clear to permit delimitation of this species. Neither holotype nor lectotype material has been designated for either *G. microcarpum* or *G. macrocarpum*, and until these species are typified, evaluation of similar taxa or varieties cannot be undertaken with any degree of precision.

In this study we address ourselves to one part of this complex taxonomic situation by choosing a lectotype for *G. macrocarpum*. Only rather vague descriptions were originally published for *G. microcarpum* and *G. macrocarpum* (Tulasne and Tulasne 1845). Tulasne and Tulasne later (1851) redescribed these species in greater detail and provided accurate line drawings of them in an article in which the genus *Glomus* was relegated to synonymy with *Endogone* Link. Bucholtz (1912) re-examined and provided spore size ranges for the Tulasne specimens of *G. macrocarpum*. He recognized the similarity of a certain Tulasne specimen (referred to as Bucholtz's No. 13) to his own collection No. 25. This last, illustrated in his Figs. 68 and 69, he considered to be the typical form intended by the Tulasnes for *G. macrocarpum*. Certain other Tulasne specimens were judged not typical by Bucholtz. When Thaxter (1922) monographed the Endogonaceae, he used the spore variation summarized by Bucholtz to substantiate his view that *G. macrocarpum* "is perhaps the most frequently observed and variable member of the genus."

The thus-established tradition of considering *G. macrocarpum* as a highly variable taxon has been perpetuated by subsequent authors (Godfrey 1957; Nicolson and Gerdemann 1968; Gerdemann and Trappe 1974; Tandy 1975; Hall 1977; Trappe and Schenck 1982). Several distinct varieties have been segregated over the same period from *G. macrocarpum* on the basis of such characters as spore wall layering and ornamentation, type of pore closure, and diameter and form of the subtending hypha. Nicolson and Gerdemann (1968) proposed two varieties of *G. macrocarpum* (var. *caledonicum* Nicol. & Gerd. and var. *geosporum* Nicol. & Gerd.) that were distinguished from the type variety in

part by their apparent (though subsequently disproved) lack of sporocarps but primarily by the morphology of their spores. Both of these have subsequently been elevated to species status. From the 12 species of chlamydosporic *Endogone* (now placed in the genus *Glomus*) that were discussed by Thaxter (1922), the number of species has risen to almost 50. Delimitation of these taxa has partly circumscribed the definition of *G. macrocarpum* by eliminating entities that are not *G. macrocarpum*.

In contrast, some of the new species described in *Endogone* have later been synonymized with *G. macrocarpum*. Thaxter (1922) considered *E. australis* Berk. and *E. pampaloniana* Bacc. to be indistinct from the variable *G. macrocarpum*. As Thaxter suspected, and as we maintain in the taxonomic section of the present paper, Thaxter's concept of a variable taxon incorporated several distinct taxa.

Gerdemann and Trappe (1974) proposed the following synonymy.

Glomus macrocarpum Tul. & Tul., *G. Bot. Ital. Part 1*, 2: 63. 1845

= *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 versiformis* Karst., *Hedwigia*, 23: 39. 1884.

= *Endogone pampaloniana* Bacc., *N. G. Bot. Ital. Part 2*, 10: 79. 1903.

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

= *Endogone guttulata* Fisher, *Schweiz. Z. Pilzkd.* 1: 85-87. 1923.

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

As a consequence of examination of the Tulasne specimens, the collections of Bucholtz and Thaxter, the type materials of most of the synonyms that have been proposed for *G. macrocarpum*, and certain of the collections cited by Gerdemann and Trappe (1974), we propose a narrowed delimitation of *G. macrocarpum*. In addition, we recognize the species status of certain previously synonymized taxa.

Consideration of some taxonomic criteria

Sporocarp

In accordance with customary usage of the term in literature on the Endogonaceae (cf. Gerdemann and Trappe 1974; Trappe and Schenck 1982), we have adopted a very general interpretation of the term "sporocarp": any primary arrangement of spores characterized by (i) the formation of a spore-enclosing hyphal

envelope and (or) (ii) the association of two or more spores formed from one or many hyphae. The term "cluster" we reserve for the specific secondary arrangement of spores within the sporocarp, as in *G. australe*, *G. fuegianum*, and *G. fasciculatum*, in which spores are grouped around a branched hypha or hyphae. Random, as in *G. macrocarpum*, and radial, as in *G. radiatum*, are two other secondary arrangements of spores within sporocarps.

Spore size

Spore size covers a range for any particular species that may overlap more or less with the range of other species. However, as a result of our more restricted concept of *G. macrocarpum*, the range of spore size has been reduced to approximately half that reported by Gerdemann and Trappe (1974).

Wall layers and laminations

Trappe and Schenck (1982) defined "wall layers" and "wall laminations" and described both the morphological features and the practical procedures for distinguishing the two. Since their theoretical and practical treatments are clear and comprehensive, we simply paraphrase their definitions for convenience of reference: "wall layers," separable or nonseparable deposits of wall material that fracture differentially when the spore is crushed to produce an edge with angular discontinuities; "wall laminations," successive, fused deposits of wall material, resulting from an intermittent process of thickening, that usually fracture as one unit when the spore is crushed.

The outermost layer of the spores of such species as *G. macrocarpum* swells in certain mounting media such as lactic acid (particularly if heated) and potassium hydroxide. We have therefore carried out all measurements of spores, once rehydrated in water, as soon as possible after mounting to minimize this problem.

Pore closure

Many spores of a given collection may have an open pore in the hypha at the point of attachment. However, in all of the taxa considered here, the pore is ultimately closed by either an occlusion or a septum. "Occlusion," as defined by Trappe and Schenck (1982), is a type of pore closure, as in *G. macrocarpum*, resulting from the inward growth of the innermost wall layer. In most cases, this is very distinct from pore closure by a septum, which as in *G. caledonicum* is normally very thin (<1 μm) and straight or somewhat curved. In certain taxa both extremes and intermediates exist.

Taxonomic section

The search through materials to be considered as possible lectotypes for *G. macrocarpum* began from a basic interpretation of what was initially intended by the Tulasnes for this taxon. The salient features of this

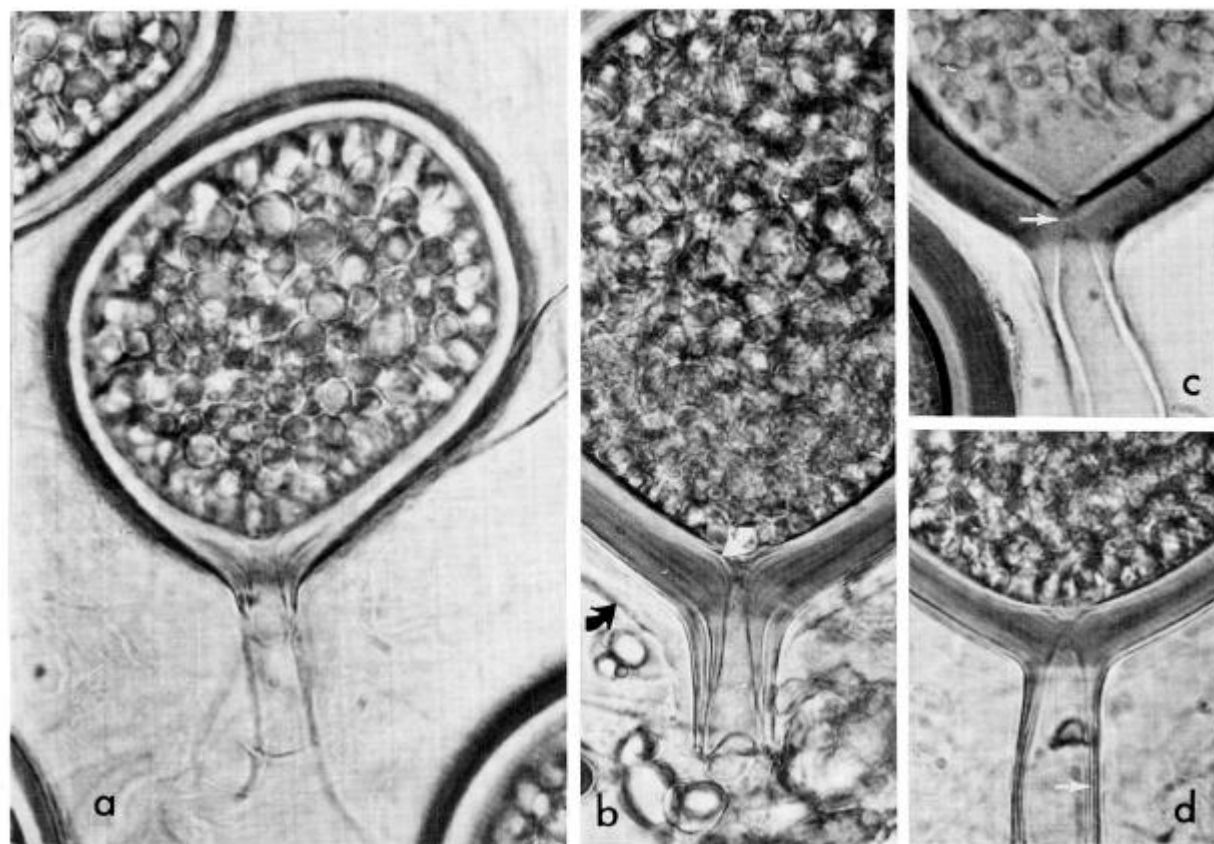


FIG. 1. *Glomus macrocarpum* Tul. & Tul. Lectotype. (a) Chlamydospore. $\times 460$. (b) Swollen outer layer of chlamydospore wall (black arrow) and laminate inner layer (white arrow). $\times 460$. (c) Occlusion of pore at point of attachment to hypha (arrow). $\times 460$. (d) Persistent subtending hypha (arrow). $\times 460$.

species, as determined from the redescription of Tulasne and Tulasne (1851), are pea- to hazelnut-sized sporocarps normally found under leaf litter or more rarely underground; peridium thin, rudimentary, or missing; spores globose or subglobose, 130–170 μm ; spore wall yellow and extending into the attached hypha.

Seven of the 11 original Tulasne collections examined by Bucholtz are now so depauperate as to be essentially useless. Two more collections seem to belong to the "thin-walled with septum" subgroup of *Glomus* (Thaxter 1922) and are similar to *G. fulvum* (Berk. & Broome) Trappe & Gerd.

Of the remaining two original Tulasne collections, one (referred to as Bucholtz No. 13) has been chosen as the lectotype. The locality of the lectotype is Chinon in the province of Touraine, France, one of the localities mentioned by Tulasne and Tulasne (1845). This particular collection was chosen as lectotype for a number of reasons: it contains sufficient material for determination; it was collected by the Tulasnes and apparently contributed to their concept of this taxon; subsequent authors, notably Bucholtz, considered it to be the typical form.

Although the spores of *G. macrocarpum* illustrated by Tulasne and Tulasne (1851) are globose or subglobose and those of the lectotype are somewhat more elongate, the range of spore shape of the lectotype includes both forms. The Tulasnes' illustrations do not show two spore wall layers, but the lectotype and all materials determined by us to be *G. macrocarpum* have two distinct wall layers. The outer wall layer is hyaline and swells more in some mountants than in others, so that under certain conditions it is difficult to discern. The pores in the subtending hyphae of the spores illustrated by the Tulasnes are not occluded, but those of all mature spores of the lectotype are.

- Glomus macrocarpum* Tul. & Tul., G. Bot. Ital. Part 1, 2: 63. 1845. Fig. 1
 = *Endogone macrocarpa* (Tul. & Tul.) Tul. & Tul., Fungi Hypogaei, p. 182. 1851.
 = *Endogone guttulata* Fischer, Schweiz. Z. Pilzkd. 1: 85–87. 1923.
 = *Endogone nuda* Petch, Ceylon J. Sci. Sect. A, Ann. R. Bot. Gard. Peradeniya, 9: 322. 1925.

Lectotype description

Sporocarps are fragmentary, none of the pieces more than 5 mm diameter.

Spores are usually slightly longer than wide, subglobose or globose, to irregular, (90–)120(–140) × (70–)110(–130) μm. Spore wall is composed of two distinct layers: outer layer is thin (1–2 μm) and hyaline when mounted in water or glycerol, usually swelling to at least twice its original thickness in lactic acid; inner wall layer is yellow in section, 6–12 μm thick, with a series of laminations occasionally visible or rarely appearing as two distinct layers, swelling relatively little in lactic acid. Spores taper to the point of attachment of the single persistent hypha. The average diameter of the hypha at this point is 16 μm. The inner wall at maturity thickens to occlude the pore of the attached hypha, and the wall thickening continues into the subtending hypha for up to 90 μm from the spore. Infrequently the pore seems to be closed by a septum that is thinner than the normal occluding wall thickening. Spores characteristically bear a straight, long subtending hypha which may extend up to 100 μm before branching or breaking.

LECTOTYPE: (PC) France, Forêt de Chinon, près Ussé, X.1841, Tulasne, determined by Bucholtz, 17.IV.1911, to be *Endogone macrocarpa* Tul., No. 13.

OTHER SPECIMENS EXAMINED: (PC) (1) FRANCE, Bois de Boulogne, près Paris, Tulasne, Bucholtz No. 6. (FH) (2) U.S.S.R., Michailowskoje, 17.VIII.1899, Bucholtz No. 25. (3) U.S.S.R., Michailowskoje, 28.VIII.1907, Bucholtz No. 26, (65+). (4) U.S.A., Kittery Point., Maine, 14.IX.1896, Thaxter, Accession No. 5205. (5) U.S.A., York, Maine, IX.1896, Thaxter, Accession No. 5206-1. (6) U.S.A., Gerrish (Is.?), Kittery Point, Maine, 16.IX.1900, Thaxter, Accession No. 5209. (7) Leponary, Patouillard, 4572. (DAOM) (8) CANADA, Ste. Foy, Quebec, 24.IX.1982, Berch. (9) CANADA, Ste. Foy, Quebec, 26.IX.1982, Berch. (OSC) (10) U.S.A., Oregon, Lane Co., 17.VI.1971, Iwan Ho, Trappe 2755, OSC 30,901. (11) U.S.A., California, Del Norte Co., 29.VI.1971, Trappe 2777-1,3,4,5,8,9,10, OSC 34,796.

Fresh sporocarps are globose, subglobose, elongate, or irregular, up to 10 × 10 × 8 mm, and have debris adherent to the surface. A thin peridium may be present on some of the sporocarp surface, but when this is absent, young and mature spores are visible at the surface. Although the sporocarp fragments in the lectotype contain little foreign matter, fresh sporocarps enclose soil particles and organic debris.

Spores in fresh and other collections are similar to those of the lectotype, but maximum spore length is 180 μm.

The types of *E. nuda* Petch (K) and *E. guttulata* Fischer (FH) have been reexamined and found to be indistinguishable from *G. macrocarpum sensu stricto*.

The type of *E. pampalonia* Bacc. has not been located and therefore cannot be considered in this study. The collection on which the name *Paurocotylis fulva* var. *zaelandica* Cooke (K-Winton 401) is based has been examined and found to contain no fungal material that corresponds to the brief description published by Cooke. Since the original description was not sufficiently detailed to define this fungus clearly, unless other authenticated material can be located, *P. fulva* var. *zaelandica* must be considered a *nomen dubium*. *Endogone australis* Berk., *E. tenebrosa* Thaxter, and *E. versiformis* Karsten, which had previously been synonymized with *G. macrocarpum*, are herein recognized as distinct species and described as new combinations in *Glomus*.

Godfrey (1957) separated some British collections of *G. macrocarpum* into four subgroups based on sporocarp and spore characters. Tandy (1975) remarked on the great variability of the South Australian and Tasmanian collections of *G. macrocarpum* but, finding that the material did not fall into distinct types, proposed no new taxa. We have found that certain Australian collections examined by Tandy should be referred to *G. caledonicum*. Hall (1977) hesitated to erect a new variety for "*Glomus* laminated spores cf. *macrocarpum*." From the published description and the colour slides of this form (I. R. Hall and L. Abbott)¹ it is clearly not *Glomus macrocarpum sensu stricto*. Nicolson and Schenck (1979) found two main forms of *G. macrocarpum* in Florida. Reexamination of all of these collections may well reveal, as in the Tulasne, Bucholtz, and Thaxter collections, other taxa misidentified as *G. macrocarpum*.

Chlamydo-spores (OSC 30,901), retrieved from pre-sterilized sand into which a plant of *Fragaria chiloensis* bearing natural mycorrhizae had been transplanted, correspond well to the morphology of sporocarpic chlamydo-spores of *G. macrocarpum*. Thus, as indicated by Gerdemann and Trappe (1974), this fungus can produce both sporocarpic and ectocarpic chlamydo-spores.

Glomus australe (Berk.) Berch, comb. nov.

Fig. 2
= *Endogone australis* Berk., in Hook., Bot. Antarct. Voy. 3: 282. 1880.

Sporocarp is reniform, 7 × 5 × 3 mm, epigeous, white when fresh according to the original description, and beige when dried. The peridium is up to 0.5 mm thick and composed of interwoven hyphae, 12–18 μm diam., that frequently branch at right angles. Sporocarp development appears to be acrogenous since younger, thin-walled spores are situated exterior to the thick-

¹Hall, I. R., and L. Abbott. Photographic slide collection illustrating features of the Endogonaceae (1979).

walled, dark spores. The sporocarp has a basal area of sterile hyphae similar to the peridial hyphae. The glebal hyphae do not form a cohesive tissue and the spores are readily teased from the cut surface.

Spores form in loose clusters which are not evident at the cut surface of the dried material. Each cluster arises from a central, branched, occasionally somewhat inflated hypha. Spores measure (120–)160(–180) μm and have two wall layers: the outer is hyaline or pale yellow, approximately 4 μm thick; the inner is light or dark brown, 7(–15) μm thick. The subtending hypha at the point of attachment to the spore is broad (20–25 μm) and thick walled. The inner wall continues into the subtending hypha for 2–40 μm and may extend into the central branched hypha of the cluster. The pore in the subtending hypha is open.

HOLOTYPE: (K) TASMANIA, Archer 34, H1804/81-1, Herb. Berk. 1879.

OTHER SPECIMENS EXAMINED: (FH) As *Endogone macrocarpa* Tul.: (1) TASMANIA, Hobart, V.1912, Accession No. 5216: 1310, 1311. (2) TASMANIA, Hobart, IV.1923, Accession No. 5218: 1313. (3) As *Endogone rodwayi* nom. ined.: TASMANIA, Rodway, Accession No. 5181. (HO) (4) TASMANIA, Cascades, VII.1919, Rodway 1310, 58252. (5) TASMANIA, Cascades, VII.1928, Rodway, 58251. (6) TASMANIA, Cascades, V.1924, Rodway, 52850. (7) TASMANIA, Newtown Creek, IV.1923, Rodway 1313, 58249. (8) TASMANIA, Near Fern Tree, V.1912, Rodway 1311, 58248.

In collections other than the type, sporocarps are reniform or irregular, up to 12 \times 10 \times 7 mm, hypogeous or epigeous. The chlamydospores are (240–)280(–325) \times (240–)290(–335) μm and have two wall layers: the outer is hyaline to light brown, 6–8 μm thick; the inner is dark brown, 8–16(–35) μm thick. The subtending hypha may be 23–65 μm broad at the point of attachment to the spore. The pore in the subtending hypha may be occluded by thickening of the inner wall layer.

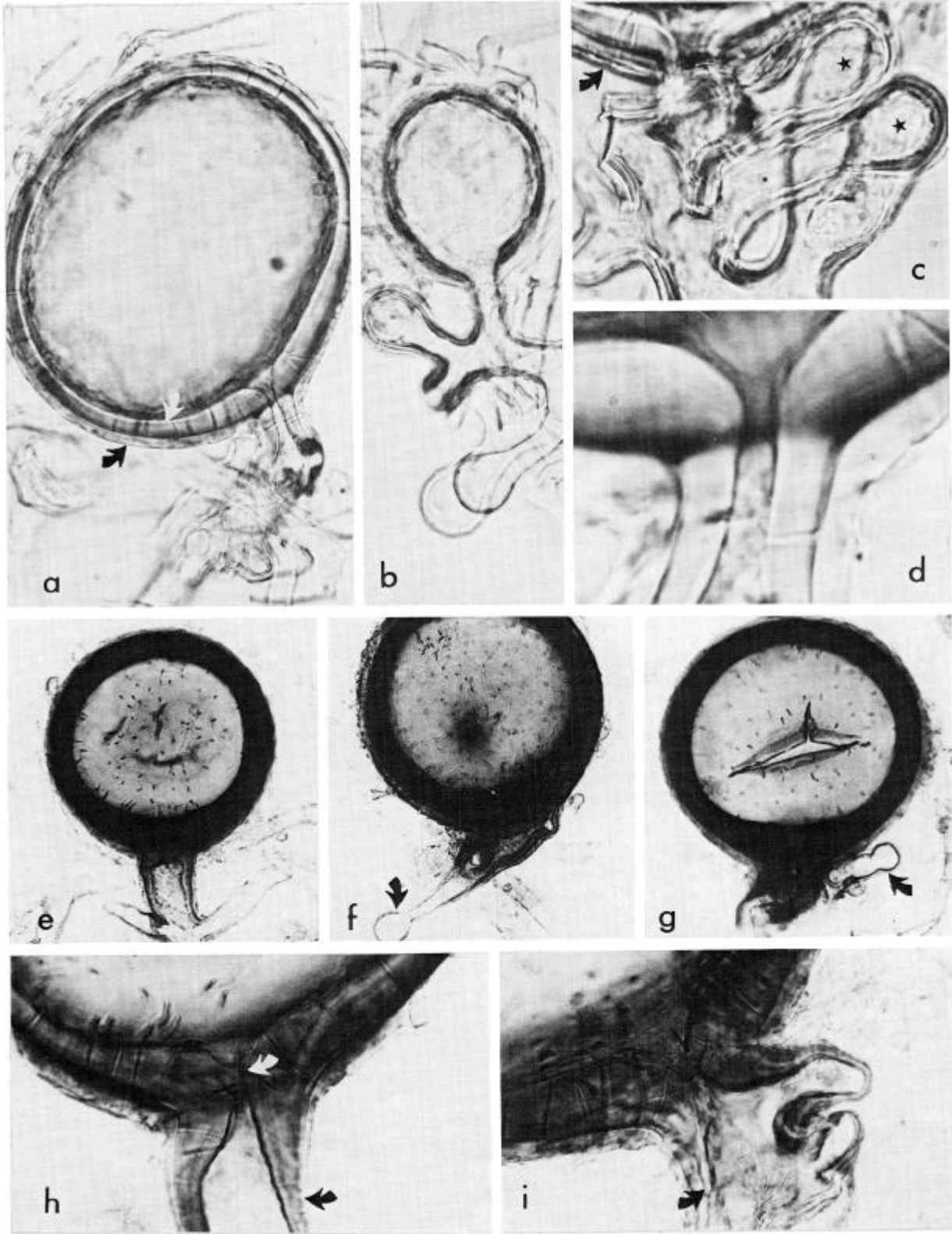
That collections of this fungus were very different from other forms of *G. macrocarpum* had been pointed out by others (Nicolson and Gerdemann 1968; Hall 1979). However, there is some disagreement over the identity of the specimens included here in *Glomus australe*. Thaxter indicated in a note to Rodway, which is preserved with Rodway's collections at HO, and on the envelope at FH containing part of Rodway's collec-

tion 1313 (Thaxter No. 5218), that the type of *G. australe* differed in having a narrower, nonflaring, subtending hypha. J. Trappe (personal communication) has also suggested that Rodway's collections may constitute a taxon distinct from *G. australe*. We have compared the range of width of the subtending hypha at the point of attachment to the chlamydospore and the range of chlamydospore size of the collections in question. These parameters do indeed vary among these collections, with the type of *G. australe* being the smallest in both respects, but the collections can be arranged in a continuum of slightly overlapping ranges based on these two characters. That these collections all belong to a single species is suggested by the following. (i) Sporocarp development in all specimens is acrogenous, with small, thin-walled chlamydospores formed at the exterior. (ii) Chlamydospores of all are formed in clusters within the sporocarp. (iii) The subtending hyphae in all collections bear laterally projecting short or swollen hyphae. When more collections have been made and examined and a better evaluation of the intraspecific variability carried out, it will doubtless be clearer whether the type specimen of *G. australe* represents a taxon distinct from the other collections or simply is a somewhat atypical example of the same taxon.

Glomus fuegianum Speg. also has spores clustered throughout the sporocarp and formed from a central, branched hypha, but the clusters are much more compact than in *G. australe*. The spores of *G. fuegianum*, as determined from the type (LPS) and the isotype (FH) materials, tend to be elongated, their shape resulting from mutual packing in the tight clusters. This is reminiscent of the situation in *Sclerocystis* spp., but in that genus spores arise from a central plexus of interwoven hyphae rather than from a single central, branched hypha. *Glomus fasciculatum* (Thaxter) Gerd. & Trappe was originally described as having spore clusters embedded in the sporocarp. The type material (FH) of this species is composed of sporocarps that disintegrate readily into clusters and individual spores, though it is unclear whether this is the mature or decrepit state of this taxon (Thaxter 1922; Gerdemann 1965).

At present, *G. australe* has been collected only from Tasmania. It is not clear whether this limited distribution will turn out to be real or a consequence of misidentification of this taxon as *G. macrocarpum*.

FIG. 2. *Glomus australe* (Berk.) Berch. (a–d) Holotype. (a) Chlamydospore showing outer (black arrow) and inner (white arrow) layers of wall. $\times 290$. (b) Young chlamydospores arising from branched hypha. $\times 290$. (c) Multibranched hypha giving rise to mature (black arrow) and immature (\star) chlamydospores. $\times 290$. (d) Open pore in subtending hypha. $\times 1050$. (e–i) Thaxter 5216:1310. (e) Mature chlamydospore with thick-walled subtending hypha. $\times 110$. (f–g) Mature and immature (arrows) chlamydospores. $\times 110$. (h) Occlusion of pore (white arrow) of thick-walled subtending hypha (black arrow). $\times 450$. (i) Mature chlamydospore on somewhat inflated hypha (arrow) with short branches. $\times 450$.



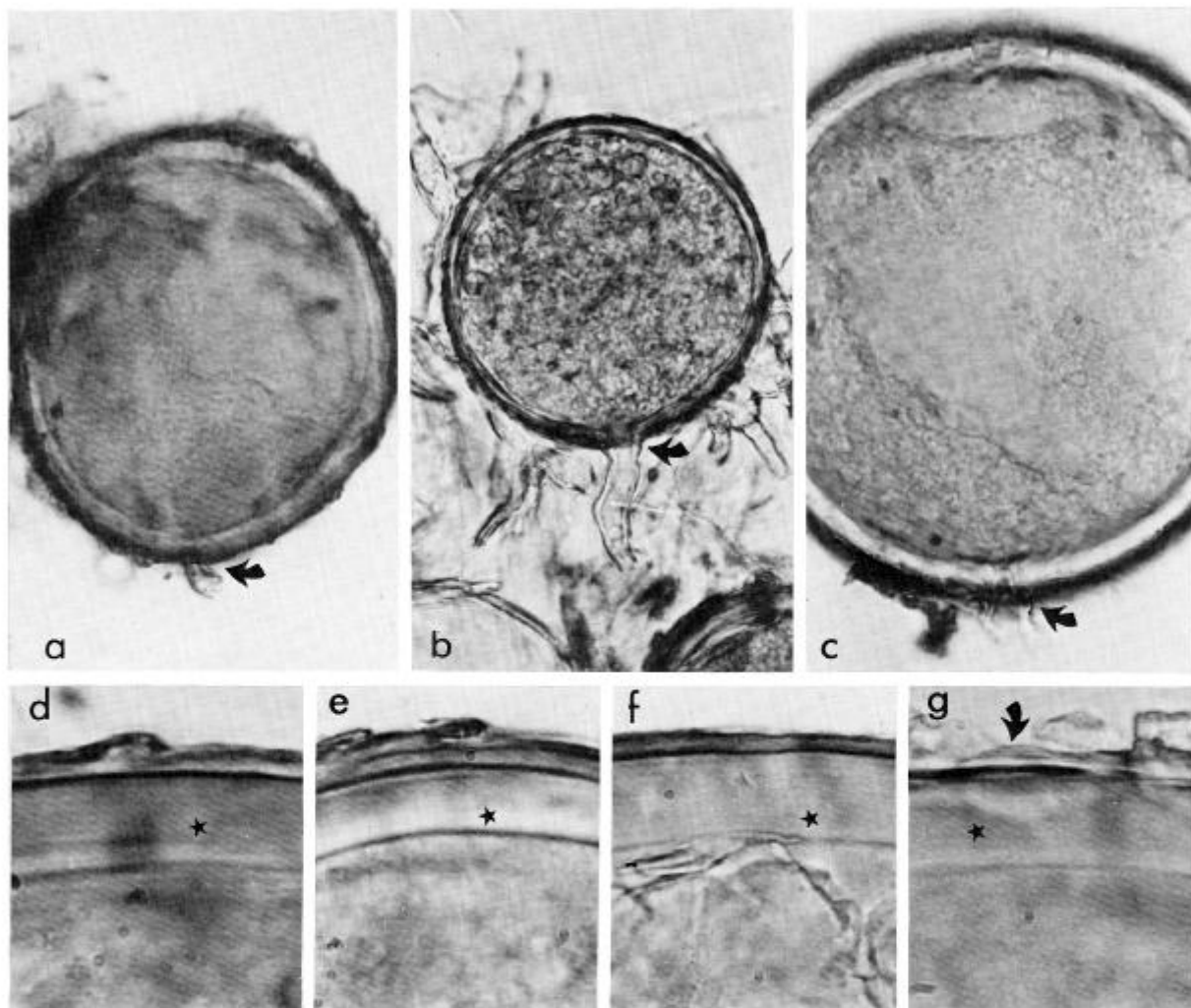


FIG. 3. *Glomus versiforme* (Karst.) Berch. (a-c) Chlamydospores with single subtending hyphae (arrows). (a) Holotype. $\times 320$. (b) Thaxter 5210-2, small-spored group. $\times 380$. (c) Thaxter 5210-1, large-spored group. $\times 380$. (d-g) Two wall layers, thin outer and thick inner (\star). (d) Holotype. $\times 960$. (e) Thaxter 5210-2. $\times 960$. (f) Thaxter 5210-1. $\times 960$. (g) Thaxter 5210-1, outer layer sloughing (arrow). $\times 960$.

Glomus versiforme (Karsten) Berch, comb. nov.

Fig. 3

= *Endogone versiformis* Karsten, Hedwigia, 23: 39. 1884.

= *Glomus epigaeum* Daniels & Trappe, Can. J. Bot. 57: 540. 1979.

Sporocarp is in fragments and yellow- or red-brown. Some debris may be incorporated, particularly in the basal region. Peridium may consist of interwoven hyphae with occasional protruding spores, or more usually is lacking.

Spores are globose, subglobose, irregular, or ellipsoid, $(125-160(-180) \times (120-140(-175)) \mu\text{m}$. Spores are dull yellow or yellow- or orange-brown with a wall

4-11 μm thick composed of a thin (1-5 μm), sloughing, hyaline outer wall adherent to a thicker (5.5-7 μm) inner wall that is yellow-brown in broken section. The sloughing outer wall layer makes the spores seem roughened. The subtending hypha is straight or recurved and occasionally may expand slightly below the point of attachment, (3-10(-13) μm wide. The subtending hypha is ephemeral, usually absent from mature spores, with a wall up to 3 μm thick at the point of attachment and tapering to approximately 1 μm within 12 μm . The pore is closed by a thin, septumlike occlusion arising from the inner wall layer.

HOLOTYPE: (H) FINLAND, Nylandia, Helsingfors (Helsinki), 23.XI.1860-I.1861, leg. Nylander, det. Karsten.

OTHER SPECIMENS EXAMINED: (H) (1) Isotype, FINLAND, Nylandia, Helsingfors (Helsinki), 23.XI.1860–I.1861, leg. Nylander, det. Karsten. (BERN) (2) POLAND, Pilsnitz bei Breslau, 1888, com. Becker, Bucholtz No. 17. (3) POLAND, Ramsern, Oderwald, 28.IX.1890, com. Becker, Bucholtz No. 20. (4) POLAND, Ramsern b. Breslau, Oderwald, 29.IX.1890, com. Becker, Bucholtz No. 23. (FH) (5) U.S.A., Botanic Garden, Cambridge, Massachusetts, 2.I.1894, Thaxter, Accession No. 5210. (6) ITALY, R. Orto Botanico, Firenze (Florence), II.1900, leg. Mattiolo, Bucholtz No. 24. (7) LATVIAN U.S.S.R., Segewold, Livland, IX.1900, Bucholtz No. 27. (HO) (8) TASMANIA, Mt. Nelson, IX.1919, Rodway, 58253. (OSC) (9) U.S.A., Oregon, Benton Co., 12.III.1970, Trappe 2133, paratype of *Glomus epigaeum* Daniels & Trappe. (10) U.S.A., Oregon, Coos Co., Allegany, 2.XII.1969, Trappe 2079. (11) U.S.A., Oregon, Lincoln Co., Five Rivers, 26.VI.1966, Trappe 603. (12) U.S.A., Oregon, Benton Co., 26.II.1944, Trappe 1810. (13) U.S.A., Oregon, Benton Co., 13.XIII.1977, Daniels, Trappe 5174, type of *Glomus epigaeum*. (14) U.S.A., California, Humboldt Co., 10.XI.1974, Ames, Trappe 4028, paratype of *Glomus epigaeum*.

In the additional collections examined, sporocarps are irregular and $8 \times 4 \times 3$ mm, and the chlamydospores are $60\text{--}195 \times 55\text{--}195$ μm . Thaxter's collection from the botanical garden in Cambridge, MA, collected during 2 years from a single potted plant, is composed of over 20 individual sporocarps which can be separated into two distinct groups. One group has large spores ($130\text{--}160\text{--}195$) \times ($110\text{--}155\text{--}195$) μm (Figs. 3c, 3f, 3g), and the other has small spores ($60\text{--}80\text{--}100$) \times ($60\text{--}75\text{--}95$) μm (Figs. 3b, 3e). The type of *G. versiforme* fits into the large-spored group; a paratype of *G. epigaeum* fits into the small-spored group; and the type of *G. epigaeum* spans an intermediate range. Although individual sporocarps tend to contain mature spores of a restricted size range, there is a unifying overlap between collections.

The herbarium packet containing the type collection of *Glomus versiforme* also contains an illustration and description of this fungus, presumably prepared by Karsten. The sporocarp is figured sitting on the substrate, the epigeous habit common for *G. versiforme*. The spores illustrated are globose and have no subtending hypha. In mature spores of all collections examined, the subtending hypha is often difficult to observe or is absent. The spores originally described in the herbarium packet and in the literature are probably immature, since the mature spores present in the type and other collections are much darker and larger.

The subtending hypha of *G. epigaeum* was described as inserted into the spore wall (Daniels and Trappe 1979). In most spores, however, the pore at the point of

attachment of the hypha appears to be closed by a fine, septumlike occlusion arising from the innermost wall layer. An ultrastructural study may be required to reveal the nature of the wall layering and occlusion of the pore.

Daniels and Trappe (1979) discussed the apparent restriction of *G. epigaeum* (= *G. versiforme*) to subtropical forests and temperate greenhouses. They felt that further collections might broaden this distribution. The type of *G. versiforme* was collected from the surface of potting soil in a greenhouse of a botanical garden at Helsinki, Finland. Thaxter (1922) collected this fungus in a botanical garden in Cambridge, MA, U.S.A., and Mattiolo's collection is from a botanical garden in Firenze (Florence), Italy. The precise sites of the collections from the regions of Breslau (Wrocław), Poland, and Segewold (Sigulda) in Latvian U.S.S.R. are not known, but these collections may extend the known geographic distribution into the northern temperate zone. In fact, contemporary collections from natural sites in Poland and Iowa, U.S.A. (J. Trappe, personal communication), and the single collection from Tasmania all indicate that *G. versiforme* is not restricted to subtropical habitats.

Glomus tenebrosus (Thaxter) Berch. comb. nov.

Fig. 4
= *Endogone tenebrosa* Thaxter, Proc. Am. Acad. Arts Sci. 57: 314. 1922.

Size and morphology of sporocarp not determinable in the type material.

Spores are globose or subglobose, ($200\text{--}240\text{--}270$) \times ($205\text{--}230\text{--}270$) μm . The spore wall is normally single, thick, ($13\text{--}18\text{--}26$) μm , and yellow to very dark brown in broken wall section, infrequently a thin (<1 μm), hyaline outer wall may be present. The thick wall may appear laminated near the subtending hypha. The outer surface of the spore is smooth or may bear flattened tubercles. The hypha is ($16\text{--}32\text{--}42$) μm at the point of attachment to the spore and fades from dark brown or yellow near the spore to yellow or hyaline within approximately 100 μm of the attachment. The pore in the subtending hypha seems to remain open, although the walls of the hypha at the point of attachment may be quite thick (up to 20 μm).

HOLOTYPE: (FH) CANADA, Little Metis, Quebec, Jeffrey No. 3.

The type collection of *G. tenebrosus* contains both dried material and material preserved in a liquid. Thaxter (1922) states that in mature spores the wall of the chlamydospore became thick and hyaline, and the spore contents dark and opaque. Examination of the original material and Thaxter's slide preparations revealed that the walls of the liquid-preserved chlamydospores had lost their colour, while those of the dried

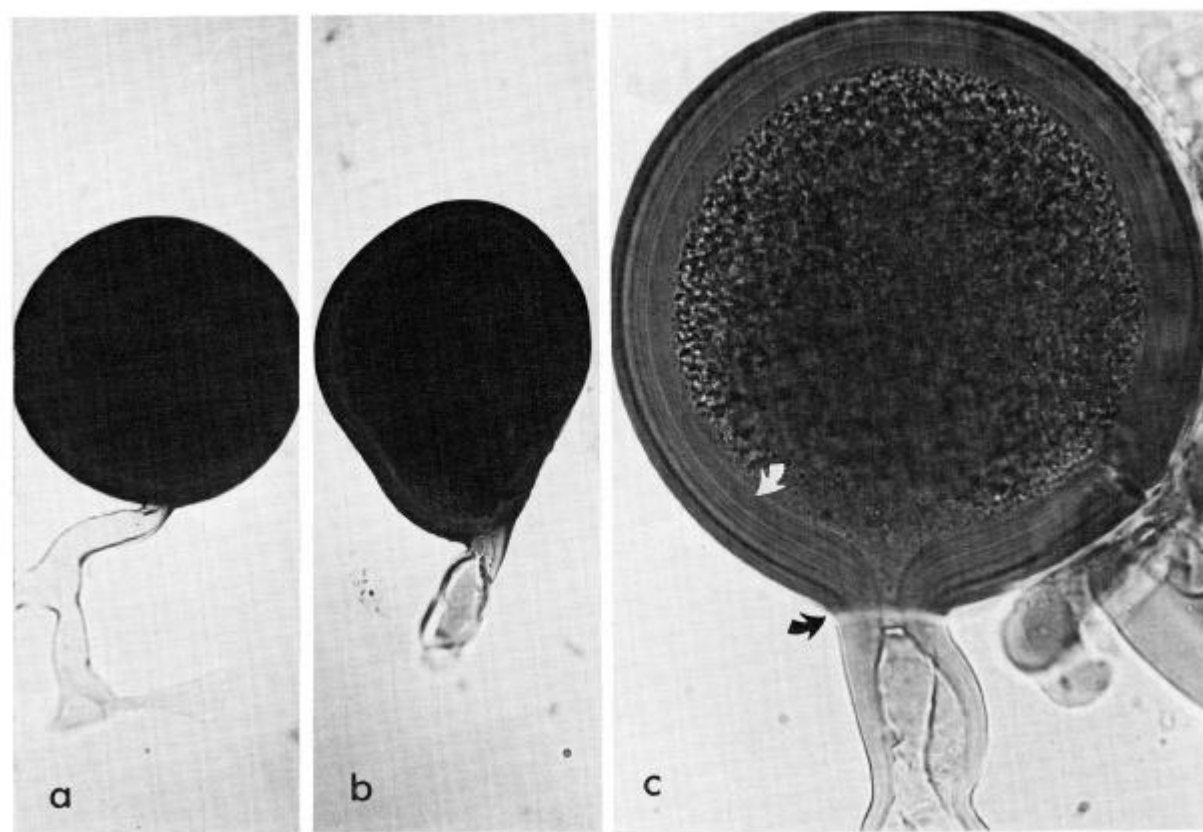


FIG. 4. *Glomus tenebrosum* (Thaxter) Berch. Holotype. (a) Dark brown, globose chlamyospore. $\times 130$. (b) Irregularly shaped chlamyospore. $\times 130$. (c) Laminated, single wall layer (white arrow) and open-pored subtending hypha (black arrow). $\times 320$.

material had remained dark brown to black. Other than this, Thaxter's description and illustration match the type material.

The large dark brown, globose or subglobose chlamyospores with thick spore wall and wide subtending hypha distinguish this species from *G. macrocarpum sensu stricto*. The chlamyospore range and colour resemble that of *G. australe*, from which, however, *G. tenebrosum* can be differentiated by the absence of spore clusters and the usually single wall layer.

Four other species of *Glomus* are known to form very dark brown or black chlamyospores: *G. constrictum* Trappe, *G. geosporum* (Nicol. & Gerd.) Walker, *G. multicaule* Gerd. & Bakshi, *G. melanosporum* Gerd. & Trappe. *Glomus constrictum* is characterized by the constriction of the subtending hypha at the point of attachment to the spore and the apparent absence of sporocarp formation. *Glomus geosporum* differs from the other dark-spored taxa in having a fine inner wall layer that forms a septum in the pore of the nonconstricted subtending hypha, a middle, and a thin outer wall layer. The rounded projections that ornament the outer spore wall surface and the normal occurrence of more

than one subtending hypha distinguish *G. multicaule*. We have examined the type material of *G. melanosporum*, the only species of these four known to form sporocarps, and confirm that the spores are distinct in bearing an envelope of fine hyphae when teased from the sporocarp and a thin-walled, ephemeral subtending hypha as described by Gerdemann and Trappe (1974). They described the spore wall as laminated, but in our observation, it appeared to be three layered.

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