TAXONOMIC CONCEPTS IN THE ENDOGONACEAE: IV. GLOMUS FASCICULATUM REDESCRIBED.

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SUMMARY

The history of and difficulties in identifying the fungus Glomus fasciculatum are discussed, the species is redescribed with a standardized terminology, and the formal description emended. Spores are pale yellow to pale yellow-brown, (50)-60-95(-149)x55-90(-149) μm, with a spore wall structure of an outer, hyaline, unit wall, 0.2-1.0(-1.8) μm thick; a pigmented, laminated middle wall (2.0)-5-10(-14.3) μm thick; and a hyaline, membranous, innermost wall 0.1-0.9 μm thick that stains red-brown in Melzer’s reagent. The subtending hypha is relatively broad, being (3.5)-9-15(-19.0) μm wide at the spore base.

INTRODUCTION

Among the described species of vesicular-arbuscular mycorrhizal fungi, Glomus fasciculatum (Thaxter sensu Gerd.) Gerd. & Trappe is perhaps the one most commonly reported from soil surveys, and most often cited as used in studies of plant growth responses (Walker 1985). It is, for example, listed 60 times in the index of the Proceedings of the Sixth North American Conference on Mycorrhizae, a figure approached only by G. mosseae (Nicol. & Gerd.) Gerd. & Trappe (Molina 1985).

Our examination of many isolates assigned to this taxon reveals confusion about the characteristics that should be used to distinguish it from other species in the genus. Very few of the fungi that we have examined correspond to Thaxter’s original type material, and it is evident that the species frequently is misidentified (Walker 1983a, 1985, 1986).

In the original description of the species (Thaxter 1922) the spores were described as being produced in small fascicles (“sporocarps”) and were “... pale yellowish or faintly brownish, mostly spherical or somewhat longer than broad, 60x60-85x70 μm ...” [p. 308].” In Fig. 27 of that publication, Thaxter illustrated (at the spore base) a thin, outermost wall layer attached to a thicker, inner wall, although no mention was made of this feature in the text.
In the 1950s, *G. fasciculatum* was reported and illustrated from soil and the stomach contents of rodents in western Canada (Dowding 1955, Bakerspigel 1956). Both authors noted the presence of a thin outer wall and a thick, laminated (“striated”) inner wall. Dowding (1955) referred to the inner wall as an “endospore” despite the fact that it was continuous with the walls of the attachment hypha.

Gerdemann (1965) examined type material of *G. fasciculatum* from Quebec and, noting that there were two collections included, designated the one labeled N:5 as a lectotype. At about the same time, he established a pot culture of a fungus which he considered to be *G. fasciculatum* (Gerdemann 1964). This fungus was described and illustrated in the 1965 paper as typical of the species, though no outer wall was noted. We have examined this material, and in our opinion it is *G. aggregatum* Schenck & Smith emend. Koske, a species frequently confused with *G. fasciculatum* (Koske 1985).

In their monograph of the Endogonaceae in the Pacific Northwest, Gerdemann & Trappe (1974) considerably expanded Thaxter’s existing description of *G. fasciculatum*. This presently seems to be the most widely used concept of the species, apparently being incorporated in a number of recent keys (Hall & Fish 1979, Trappe 1982, Hall 1984). The spores were described as “... 35-105 μm diam when globose, 75-150x35-100 μm when subglobose to obovate, ellipsoid, sublenticular, cylindrical or irregular... spore walls highly variable in thickness (3-17 μm) hyaline to light yellow or yellow brown... hyphal attachments 4-15 μm, occluded at maturity. Walls of attached hyphae often thickened to 1-4 μm near the spore [p. 51].” Spores were not illustrated or figured, and no mention was made of a thin, outermost wall. This is an extremely broad description and it was recognized that “... a more intensive study of the relationships within this group is needed ... [p. 53].”

*Glomus fasciculatum sensu lato* has now been shown to include several distinct taxa, some of which (e.g., *G. deserticola* Trappe, Bloss & Menge, *G. aggregatum*, and *G. hot* Berch & Trappe) have been named (Schenck & Smith 1982, Trappe, Bloss & Menge 1984, Koske 1985, Berch & Trappe 1985). Since 1974, the importance of spore wall characteristics in the taxonomy of the Endogonaceae has been increasingly recognized (Trappe & Schenck 1982, Walker 1983b, 1986), and such criteria were of major significance in segregating new species from *G. fasciculatum sensu lato*. However, the spores of *G. fasciculatum sensu stricta* have not been adequately redescribed or illustrated to show the features now considered to be important identifying characteristics.

The following redescription of *G. fasciculatum sensu stricta* is based upon examination of Thaxter’s sporocarpic material from the Farlow Herbarium, another collection from the type locality, Little Metis, Quebec, made in 1983, and 11 other collections made from several different parts of the world. Despite its wide distribution, the species has spores that show a high degree of consistency in morphology, and the taxon is clearly defined and stable, indicating that the large range of morphology previously attributed to it was due to taxonomic error, rather than to phenotypic instability or variation.
Terminology for features of spore wall structure follows that of Walker (1983b). Descriptions are made from spores in mounts based on polyvinyl-alcohol, with (PVL) and without (PVLG) phenol (Walker 1979, Koske & Tessier 1983), standard mounts we generally use for all our taxonomic descriptions. Thaxter's material was preserved in an unidentified fluid, and is in very poor condition (Fig. 1).

Nonetheless, it proved possible to make microscope slide mounts in which essential features were still evident (Fig. 1). Other collections were preserved either in lactophenol, which usually changes the color of endogonaceous spores (Gerdemann 1965, Hall 1984, Koske & Walker 1985), or in 5% aqueous formaldehyde solution, which preserves color better, but which tends to render the spores brittle and may result in fusion of adjacent walls (Koske & Walker 1986). Voucher collections have been deposited in the Farlow Herbarium (FH), or the Herbarium of Oregon State University (OSC). Measurements given are from a total of 177 spores from eight different collections.

**SPECIES DESCRIPTION**


Figures 1-3.

Sporocarps hypogeous or epigeous, up to 1 mm diam, irregularly globose or flattened, sometimes tuberculate, pale yellow to pale yellow-brown; peridium lacking. Spores, (50-160-95-149)×55-90(-149) μm, formed singly in the soil, in loose aggregations, compact clusters, or sporocarps; globose, subglobose, sublenticular, or occasionally irregular; pale yellow to pale yellow-brown. Spore wall structure (see murograph, Fig. 3) of three walls (1-3) in one group (A). Wall 1 smooth, hyaline unit wall, 0.2-1.0(-1.8) μm thick. Wall 2 pale yellow to pale yellow-brown, laminated, (2.0-)5.0-10.0(-14.3) μm thick. Wall 3 a hyaline, membranous wall, 0.1-0.9 μm thick, adherent to wall 2, staining red-brown in Melzer's reagent. Subtending hypha (6-)33-75(-260) μm long, often paler in color than the spore, flared, straight, or slightly constricted proximally, (3.5-)9.0-15.0(-19.0) μm broad at the spore base with walls 3-6(-8) μm thick proximally, tapering to 1.5-2.0 μm thick distally. Pore open, or closed by thickening of wall 2.

**COLLECTIONS EXAMINED**

1. LECTOTYPE: CANADA - Quebec Province, Matane County, Little Metis; in sphagnum moss (Collection N:5 of E. C. Jeffrey)(FH 5048). OTHER COLLECTIONS:
2. CANADA Quebec Province, Matane County, Little Metis; in sphagnum moss (Koske 533, Walker 653); 3. USA - California, Santa Barbara County (Koske 579); 4. Massachusetts, Bristol County from J. Gemma (Gemma 05-48-23); 5. Rhode Island, Washington County (Koske 475, 10A, Walker 650); 6. Iowa, Ames, in pot culture with *Zea mays L.*, origins unknown (Walker 316); 7. Oregon, Benton County (OSC 30456, 30967); 8. Jefferson County (OSC 30455); 9. Lincoln County
(OSC 30823); 10. Nevada, Reno, in mixed pot culture with Glomus clarum Nicol. & Schenck from Dr. G. Bethlenfalvay (Walker 779); 11. Washington, San Juan County (OSC 32390); 12. UK - Scotland, Borders Region, Manor Valley, from upland pasture (Walker 290); Midlothian, Bush, from mixed grasses and forbs (Walker 780); 13. ITALY - Torino, Botanical Gardens, in pot culture with Allium porrum L., from Dr. V. Gianinazzi-Pearson, INRA, Dijon, France (Walker 1161).

DISCUSSION

*G. fasciculatum sensu stricta* is distinguished from other species by its spores which are pale yellow to pale yellow-brown in color with a somewhat broad, thick-walled subtending hypha, and which have a spore wall structure of three walls in a single group. The thin, outermost wall is visible in most specimens (Fig. 2) and is persistent, though it may be very thin and difficult to see even at high magnifications. The laminated wall 2 typically is 5-10 μm thick, but may be much thinner (∼2 μm), and occasionally may be almost 15 μm in thickness. Wall 3 is difficult to observe in fresh, unstained spores, although it is revealed by its reaction to Melzer’s reagent, application of which causes it to become dark red-brown. After a few hours in this reagent, the reaction begins to spread into wall 2. Wall 3 does not form a complete endospore, but apparently is continuous with the subtending hypha.

When spores were left in soil in a plastic bag for 2 years at 5°C, wall 3 became easily visible, even in unstained spores, because it separated from wall 2 and collapsed when mounted in PVL or PVLG. The appearance of these spores was almost identical to some of the specimens in Thaxter’s type material, although in much of the type, wall 3 is difficult to discern.

The color of spores of *G. fasciculatum* varies from pale yellow to very pale yellow-brown. We have never observed either brown or red-brown spores of this species, except when preserved in lactophenol or FAA (both substances cause the walls to

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**Fig 1**: *Glomus fasciculatum*. Chlamydomspores from the original type material used by Thaxter (1922) in his protologue description. Most of the type material is in a very poor state of preservation.

A) Sporocarpic spores densely embedded in a hyphal matrix.
B) Fascicle of spores.
C) Individual spores dissected from a sporocarp. Note subtending hypha (arrow).
D) Spore with inner, membranous wall (m) indicated.
E) Spore with subtending hypha closed by spore wall thickening (large white arrow). Wall 1 is particularly evident where it has broken away slightly from wall 2 near the spore base (small black arrow).
F) Unit wall (1) separated from laminated wall (2) in a crushed spore. Membranous wall (3) is visible because of its wrinkling.
G) Lamination in wall 2 (large arrow). Note open lumen in the subtending hypha (see also Fig. 2C).
H) Spore showing wrinkling of wall 3 as a result of poor preservation.
I) The subtending hypha of this specimen is (unusually) constricted at the spore base (arrow).
darken considerably). Neither have we seen hyaline or white spores of *G. fasciculatum*. In all the living cultures we have examined, even the youngest spores are pale yellow.

The subtending (attachment) hypha of *G. fasciculatum* spores usually is persistent, straight, with relatively little taper, and slightly paler in color than the spore itself. The pore of the hypha may be open, or may be closed by thickening of wall 2 (Fig. 2C, 2F), but it is never closed by a septum.

We have recovered *G. fasciculatum* from soil as single spores, as spores in compact clusters, and as small sporocarps (lacking a peridium) which are between 250 μm and 1 mm across. Such sporocarps lack a structured peridium, and may incorporate fragments of the substrate such as sand grains. The color of the sporocarps we have examined varies from pale yellow to pale yellow-brown, in contrast to that reported by Gerdemann (1965) which was “light cream”. Sporocarp dimensions listed in the redescription of Gerdemann & Trappe (1974) were up to 8x5x5 mm, although, because of the broad interpretation of the species in that publication, it is impossible to be sure of the identity of the specimens used to obtain these measurements. Since Thaxter’s (1922) descriptions of sporocarps were made from a mixed collection containing *Endogone* and *Tuber* spp. as well as *G. fasciculatum* chlamydospores (Gerdemann 1965), it is impossible to be sure how large the sporocarps in the collection were. It is our opinion that, for this species, sporocarp dimensions are not reliable taxonomic characteristics. It is sufficient to know that spores of this fungus can be found either singly, in loose clusters, or in dense aggregations that can be described as sporocarps.

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**Fig. 2:** *Glomus fasciculatum*. Recent collections, numbered as in 'Collections Examined' in text.

A) A loose cluster of spores from collection 13. The contents of the crushed spores appear as globules in the mounting medium.

B) Detail of a portion of the cluster in A. The three walls are indicated (1, 2 & 3).

C) Intact spore from the cluster in A. The lumen of the subtending hypha has been constricted by ingrowth of the walls (arrowed).

D) Crushed spore from collection 13 showing all three walls. The collapse of wall 3 reveals its membranous nature.

E) Fascicle of spores recovered from collection 2.

F) Spore from collection 2. All three walls are visible. Note the partial closure of the lumen of the subtending hypha by spore wall thickening.

G) Spores from collection 5. The spore in the lower right of the photograph is parasitized. The membranous inner wall (wall 3) is wrinkled. The outer wall (wall 1) is arrowed. Note unusually thick laminated wall 2.

H) Crushed spore from collection 5. Wall 3 has not separated in this specimen, but has stained darkly in Melzer’s reagent.

I) Spores in roots from collection 10.
In our experience, *G. fasciculatum* is not common. It is likely that many isolates of other fungi have been erroneously identified as *G. fasciculatum* and used in published studies. Because of this, the interpretation of the literature is difficult, if not impossible. Few voucher specimens have been lodged, and it often is impossible therefore to verify identification. In a sample of 10 collections from those examined by Gerdemann & Trappe for their redescription, only five (Trappe numbers 30455, 30456, 30823 (part), 30967 and 32390) coincided with our concept of *G. fasciculatum*. The remaining specimens were either undescribed, or were species (*G. aggregatum, G. hoi* or *G. intraradices*) that have been described since 1974. Other species we have examined that have been commonly misidentified as *G. fasciculatum* include *G. deserticola*, *G. invermaium* Hall, *G. feugianum* (Specazzini) Trappe and Gerd., *G. occultum* Walker, *Sclerocystis rubiformis* Gerd. & Trappe, and several other undescribed species. The Rothamsted isolate often known as E3 and frequently cited as *G. fasciculatum* is definitely not that species, and is undescribed.

At present, because they are poorly known, it is impossible to describe all of the species that have been confused with *G. fasciculatum* or to differentiate them from each other and from *G. fasciculatum sensu stricto*. Our intent has been to establish a new, clarified description of the species from which further studies can be made as appropriate. *Glomus fasciculatum* is clearly defined by the characteristics described and discussed here, which may be summarized as follows:

**Glomus fasciculatum**

HAS

* BOTH ECTOCARPIC AND SPOROCARPIC SPORES
* SPORES 50-149 × 55-149 μm IN SIZE
* SPORES WHICH MAY BE QUITE VARIABLE IN SHAPE, BUT WHICH USUALLY ARE GLOBOSE TO SUBGLOBOSE
* SPORES WITH A WALL STRUCTURE OF:
  - a thin, hyaline outer unit wall
  - a thicker, yellow to pale yellow-brown middle laminated wall
  - a thin, hyaline, inner, membranous wall [the muronym (Walker 1986) is A(ULM)]
* A REACTION TO MELZER’S REAGENT. THE INNER WALL TURNS RED

DOES NOT HAVE

* BROWN OR RED CHLAMYDOSPORES
* HYALINE CHLAMYDOSPORES
* ONE- OR TWO-WALLED SPORES
* SPORES WITH CONTENTS OCCLUDED BY A SEPTUM
* SPORES LESS THAN 50 μm DIAMETER
Fig. 3: Murograph (after Walker 1983) of *Glomus fasciculatum* sensu Walker & Koske. Wall 1 is a unit wall, wall 2 is a laminated wall, and wall 3 is a membranous wall. Asterisks indicate that the walls may be difficult to see. The muronym (Walker 1985) is A(ULM)

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LITERATURE CITED


