Taxonomy of *Acaulospora gerdemannii* and *Glomus leptotichum*, synanamorphs of an arbuscular mycorrhizal fungus in Glomales

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Comparison of type specimens of *A. gerdemannii* and *A. appendicula* revealed the spores to be identical in organization and subcellular structure, indicating they are conspecific. The *Glomus* morph of *A. appendicula* was not assigned a name in the protologue, but 11 living cultures started from or producing spores of *A. gerdemannii* also generated *Glomus*-like spores of identical morphology to those in type specimens of *Glomus leptotichum*. These spores were indistinguishable from those in type specimens of *G. fecundisporum*, indicating they are conspecific. Both species were described in the same paper, so the name *G. leptotichum* is given priority because type specimens are in better condition and specimens from a reference culture have been identified by an author of both prologues. Absence of a teleomorph and confirmation of dimorphism from single and multiple-spore inoculations of host plants in culture provide the basis for designating *A. gerdemannii* and *G. leptotichum* as synanamorphs of one vesicular-arbuscular mycorrhizal fungus.

Acaulospora appendicula Spain, Sieverd & N. C. Schenck, in the Acaulosporaceae (Glomales) (Morton & Benny, 1990) is unique among the described species known to form vesicular-arbuscular mycorrhizas. It is reported to produce spores of two distinct morphotypes (Schenck *et al.*, 1984), one morphotype resembling those of other species in *Acaulospora* and the other morphotype resembling those of species in *Glomus* (Glomaceae). The *Acaulospora*-like spores develop laterally from a hypha that first inflates terminally to differentiate a 'sporiferous saccule' (Morton, 1988). Unlike most other *Acaulospora* spp., however, these spores develop on an obvious branch (or 'pedicel') arising from the saccule hypha, a *Glomus*-like feature. Schenck *et al.* (1984) assigned primacy to the *Acaulospora* morphotype in determining the taxonomic position of the species. Spores of the *Glomus* morphotype were given little taxonomic attention and they were not compared to other known species.

Only in the protologue of *A. appendicula* was any suggestion made of the species producing spores of two morphologies that encompass two genera (Schenck *et al.*, 1984), each of which later was placed in a separate family (Morton & Benny, 1990). Schenck *et al.* (1984) did not provide empirical evidence to demonstrate the common origin of both morphotypes, nor were any isolates known from other geographic locations to ascertain stability of dimorphic reproductive behaviour.

Examination of type specimens of different *Acaulospora* spp. at the Oregon State University Herbarium (OSC) revealed close correspondence in subcellular organization and structure of both spores and saccules of *A. appendicula* and *A. gerdemannii* N. C. Schenck & T. H. Nicolson. A broader comparison among isotypes from Florida (FLAS) revealed that the *Glomus*-like spores of *A. appendicula* were identical to those in a reference culture (FL184) of *Glomus leptotichum* N. C. Schenck & G. S. Sm. accessed in the International Collection of Arbuscular and Vesicular-Arbuscular Mycorrhizal Fungi (INVAM). Comparisons of OSC and FLAS type specimens also showed insignificant differences between *G. leptotichum* and *G. fecundisporum* N. C. Schenck & G. S. Smith.

In this paper, documentation is presented to synonymize *A. appendicula* with *A. gerdemannii* and *G. fecundisporum* with *G. leptotichum*. Experiments provide strong evidence that *A. gerdemannii* and *G. leptotichum* should be classified as synanamorphs (two or more anamorphic states of the same fungal organism). Each synanamorph is redescribed using the character terminology first proposed by Walker (1983) and expanded by others (see Morton, 1988) until development studies are completed.

MATERIALS AND METHODS

INVAM accessions were chosen which concurrently produced spores of *A. gerdemannii* and *G. leptotichum*. They included BR229, FL130A, NC169, NC171, NC176, VZ856, and WV109C. Other accessions chosen because they produced mainly spores of *G. leptotichum* included FL184, MX982A, NG107C and NI108. Cultures of all accessions were produced according to protocols described by Morton

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et al. (1993). Briefly, each pot culture consisted of whole inoculum (roots, growth medium, hyphae, spores) diluted 1:10 (v/v) with a soil medium, seeded with *Sorghum sudanense* (Piper) Staph., and grown in a greenhouse for four months. The soil medium consisted of two parts #3 quartzite sand (mean particle size of 0·9 mm) and one part soil (Lily series, 0·9% organic matter, pH adjusted to 6·2 with calcium carbonate, 8·0 mg kg^{-1} bicarbonate extractable phosphorus). Cultures were grown for four months in a greenhouse, dried *in situ*, and then stored at 4 °C (temperate isolates) or 20° (tropical isolates).

Spores of *A. gerdemannii* and *G. leptotichum* from cultures of FL130A, NC171, and WV109C were hand-picked and separated using a glass pipette extruded to a fine tip. Populations of 50–100 spores of each species were pipetted along the length of roots of 10-day-old *Sorghum vulgare* L. seedlings that were then immediately transplanted into 4 × 21 cm Cone-tainers™ (Stuewe & Sons, Corvallis, Oregon). After four months, cultures were harvested and stored at 4° until used. Some cultures also were started with single spores of *G. leptotichum* hand-picked from a culture of INVAM accession NC176 using the same protocol.

Spores were extracted from all cultures by wet-sieving and decanting followed by sucrose gradient centrifugation (Daniels & Skipper, 1982). Spores were washed and collected individually using a pipette with a finely extruded tip. Spore size was measured with an ocular micrometer and colour quantified from a printed colour chart (INVAM colour chart, available from the senior author). The colours on the chart were composed of various percentages of the component colours: cyan, magenta, yellow and black (C–M–Y–K). A two-branch fibre optic illuminator (colour temperature 3400 °K) was used to illuminate the spores and colour chart simultaneously. Mounted broken spores were examined with a Nikon Optiphot compound microscope equipped with differential interference contrast (DIC) optics.

Voucher specimens of whole and broken spores were prepared and deposited in the INVAM slide collection and are available for loan upon request to the senior author. Samples of 200–500 spores from each culture were placed in vials containing 0·05% sodium azide and stored indefinitely at 4°. Another sample of 50–100 spores from each culture were mounted permanently on glass slides in polyvinyl alcohol-lactic acid-glycerol (PVLG, Koske & Tessier, 1983) and PVLG mixed with Melzer's reagent (1:1 v/v).

Additional cultures of reference accessions INVAM FL130A (both species sporulating) and FL184 (*G. leptotichum* sporulating) were started using the same protocol described earlier, except that *Zea mays* L. was seeded as the host plant. Roots were sampled 45 days after emergence, stained in 0·05% trypan blue using the protocol of Koske & Gemma (1989), mounted permanently in PVLG, and mycorrhizal morphology examined under a compound microscope.

RESULTS AND DISCUSSION

No evidence exists to indicate that spores of *A. gerdemannii* and *G. leptotichum* are teleomorphic states. At present, all fungi in *Acaulospora* and *Glomus* are thought to be obligate anamorphic species (Morton & Benny, 1990). Four separate lines of evidence affirm that both species are anamorphs of the same fungus, and therefore can be classified as synanamorphs. First, spores of both species were produced concurrently in cultures of NC176 started with single spores of *G. leptotichum*. Inoculations with multiple spores of each species from accessions FL130A and NC171 also produced cultures with both species sporulating concurrently. Secondly, hyphal strands were collected which connected a spore of *G. leptotichum* with a saccule or saccule and spore of *A. gerdemannii* (not shown). Thirdly, geographically separated isolates from three continents produced spores of both species in successive propagation cycles, but the proportions of each varied considerably among accessions. Both species were consistently present in cultures of BR229, FL130A, NC169, NC171, and WV109C (Fig. 1). Cultures of VZ856 initially consisted only of *A. gerdemannii* spores, but spores of *G. leptotichum* appeared and increased with successive cycles. A culture of NG107C started with spores of *A. gerdemannii* yielded only spores of *G. leptotichum* after one propagation cycle. Cultures FL184, MX982A, and NI108 were started with spores of *G. leptotichum* and yielded spores of the same species and infrequent spores of *A. gerdemannii*. Fourth, mycorrhizae of cultures with both species (FL130A) were identical to those of a culture containing only *G. leptotichum* (FL184).

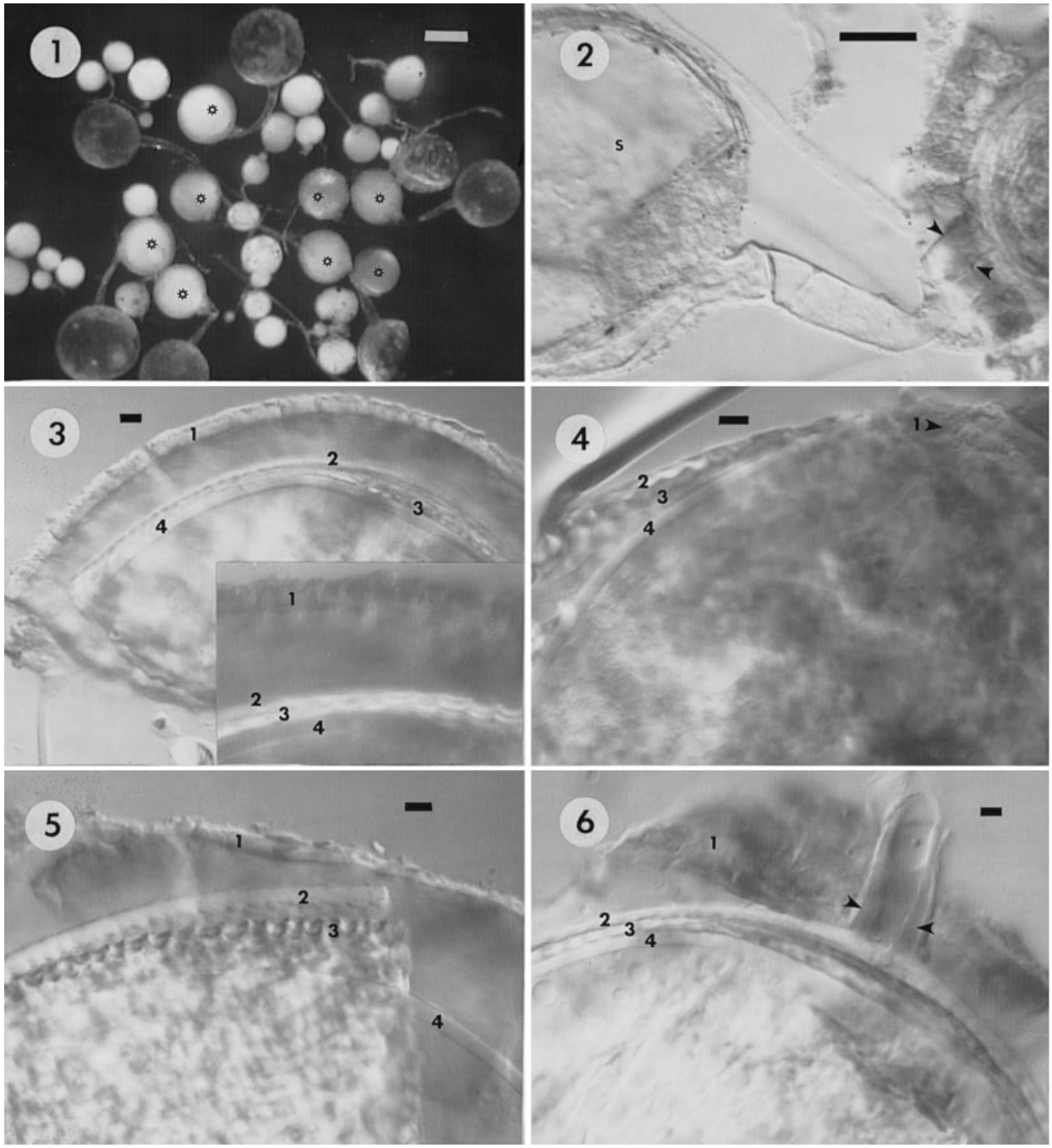
The unnamed *Glomus* morphotype in the protologue of *A. appendicula* (Schenck *et al*., 1984) was identified as *G. leptotichum* based on correspondence in morphology of type specimens of both species. In addition, one parasitized spore of *A. gerdemannii* was found on slides of holotype (OSC 40,429) and isotype (FLAS F52577) specimens of *G. leptotichum*. No mention of these spores was made in the protologue (Schenck & Smith, 1982), suggesting they were rare and not detected in the cultures from which the type specimens originated.

Separate species names for both synanamorphs is a necessary convenience since cosporulation is much rarer in nature than in greenhouse pot cultures. For example, only spores of *A. gerdemannii* were recovered from soils sampled in Mexico (Berch, Ferrera-Cerrato & Chavez, 1989), La Gran Sabana, Venezuela (Cuenca & Lovera, 1992), the Cedar Creek region in Minnesota (Johnson *et al*., 1991), and the states of Pernambuco (Maia & Trufem, 1990) and Minas Gerais (Siqueira, Colozzo-Filho & de Oliviera, 1989) in Brazil. Conversely, only *G. leptotichum* spores (reported as *G. fecundisporum*) were found in soils from Neyveli, India (Ganesan *et al*., 1991), New Jersey and Virginia sand dunes (Koske, 1987), and Kentucky pastures (An *et al*., 1993). Koske (personal communication) provides the only report of cosporulation by both synanamorphs in the University of Rhode Island turfgrass plots.

Synanamorph

Acaulospora gerdemannii N. C. Schenck & T. H. Nicolson. Mycologia **71**, pp. 193–194. (1979).
= *Acaulospora appendicula* Spain, Sieverd. & N. C. Schenck. Mycologia **76**, pp. 686–689. (1984).

We conclude that *Acaulospora gerdemannii* and *A. appendicula* are conspecific, based on correspondence of subcellular organization and structure of spores and of attached saccules



Figs 1–6. *Acaulospora gerdemannii* **Fig. 1.** Spores (with asterisks), together with those of *Glomus leptotichum*, in a culture of INVAM WV109C; bar = 200 μm. **Fig. 2.** Spore with attached pedicel (arrows) branching from the hypha bearing a terminal saccule(s), from slide of the isotype of *A. appendicula* (FLAS F53,673); bar = 50 μm. **Fig. 3.** Broken spore from a slide of the holotype of *A. appendicula* (OSC 41,495), showing all four walls (1–4), insert shows more detail of scalloped ornamentations on walls 2 and 3; bar = 10 μm. **Fig. 4.** Partially degraded broken spore from a slide of the holotype of *A. gerdemannii* (OSC 37,514), showing all four walls (1–4); bar = 10 μm. **Fig. 5.** Broken spore freshly extracted from INVAM accession FL130A and mounted in PVLG + Melzer's reagent (1:1 v/v), with all four walls (1–4) clearly visible; slide # 1884; bar = 10 μm. **Fig. 6.** Broken spore freshly extracted from INVAM accession FL130A and mounted in PVLG + Melzer's reagent, showing the continuity of walls 1 and 2 into the pedicel (arrows) and an 'endospore' formed by walls 3 and 4, slide # 1539; bar = 10 μm.

in type specimens. The structure and properties of all subcellular structures seen in the types were verified in fresh spores extracted from actively growing cultures. The name *A. gerdemannii* is assigned priority based on date of publication.

The terminal saccule from which a spore originates is described as 190–380 μm and 290–365 μm diam. in the protologues of *A. appendicula* and *A. gerdemannii*, respectively. Saccules in INVAM culture accessions are 220–340 μm, encompassing the range of both species. The saccule wall appears to consist of only one layer, 3–7 μm thick, that degrades in patches on the surface and appears flakey (Fig. 2).

The reported range in spore size was narrower for *A. gerdemannii* (200–250 μm) than for *A. appendicula* (170–390 μm). Spores from cultures of FL130A, NC171,

WV109C overlapped both described species (160–300 μm, $n = 220$), with a mean diam of 192 μm.

Spores of *A. gerdemannii* are reported as brown (Nicolson & Schenck, 1979) whereas those of *A. appendicula* are described as dull yellow-cream to orange-tan (Schenck *et al*., 1984). Newly-formed spores from active cultures range in colour from white (outer walls sloughed) to pale cream (0–0–15–0) (Fig. 1), but they become a darker yellow-brown (0–10–40–0) or pale orange-brown (0–40–100–0) after storage for one year or longer. Parasitized or spores with accelerated senescence are dark orange brown (0–40–100–10) to brown (20–60–100–10). The effects of spore age, culture conditions, and storage duration on spore colour are not documented in either protologue, but most spores in the holotype and isotype specimens of *A. gerdemannii* were so degraded that either prolonged storage or parasitism could account for the darker colour reported.

Subcellular organization in spores of *A. appendicula* was reported to consist of four distinct 'walls' in two separable groups, whereas that of *A. gerdemannii* spores was described as consisting of only two walls. However, spores of both type specimens were identical in structure and organization (Figs 3–4) that matched the description of *A. appendicula*. Spores of all INVAM cultures were identical in morphology to those of type specimens of both species, with all subcellular structures intact (Figs 5–6).

The outer wall is a fragile structure that varies in appearance with age, ranging from 6–20 μm thick depending on amount of deterioration or breakage. On newly-formed spores, it is a cream (0–20–40–0) to orange-brown (0–40–100–0) colour. This wall appears loosely structured, with deep fissures visible on the surface that serve as fracture points when pressure is applied. On aged spores from stored cultures or from field soil, this wall appears to develop cerebriform folds or it sloughs completely from the spore, as described in the protologue of *A. gerdemannii*. These folds can harden with time and appear rigid on spores stored in lactophenol or mounted in PVLG. Such hardened folds were found on spores of the *A. gerdemannii* type and on spores of VZ856 stored in pot culture medium for two years at 4°. This wall stains a pale to dark red–brown colour when placed in Melzer's reagent, as described for *A. appendicula*. Intensity of the staining reaction is greatest in newly formed spores and declines as spores age. No mention was made of a reaction in *A. gerdemannii* spores, and type specimens were too degraded to be tested.

The second wall is rigid, hyaline, 2–6 μm thick, and continuous with the wall of the 'pedicel'. It is present in some spores of both type specimens, but otherwise is absent (often along with the outer wall when it sloughs). This wall has hemispherical protruberances 1–2 μm high along the inner surface that Schenck *et al*. (1984) describe as forming an 'alveolate reticulum'.

The third wall circumscribes a true 'endospore' because it is continuous and has no physical connection with the first two walls in mature spores. It is rigid, 4–8 μm thick, and ornamented with numerous concave hemispherical depressions 1–2 μm deep on the outer surface. These depressions cause considerable light scattering in reflected light, as seen in photographs of both protologues as well as in type specimens mounted on slides (Figs 3–4). These ornamentations were described by Schenck *et al*. (1984) as an 'alveolate reticulum'.

The fourth wall separates readily in fresh spores from all other walls and is hyaline, smooth, somewhat flexible and bilayered. The outer layer is not mentioned in either protologue, even though it is visible in type specimens. This layer is < 1 μm thick and is detectable in broken fresh spores only when it separates slightly from the much thicker (4–8 μm) inner layer. The only other arbuscular fungal species with spores having a similar flexible inner wall is *Entrophospora infrequens* (I. R. Hall) R. N. Ames & R. W. Schneid. (INVAM reference culture AZ237) (Morton, unpublished).

The pedicel bearing a spore that branches from the hypha subtending the saccule (Figs 2, 6) is described in the protologue of *A. appendicula*. It is not mentioned in the description of *A. gerdemannii*, although it is visible on at least one spore of the holotype and in Fig. 3 of the protologue. The pedicel wall is continuous with the second wall of the spore and appears to partition the spore contents with a thick septum (Fig. 6).

Mycorrhizas from INVAM accession FL130A (producing both synanamorphs) consisted of coiled and knobby hyphae 3·5–8 μm in diam and finely branched arbuscules in cortical cells of 30 day-old mycorrhizal maize roots (Fig. 7). The staining reaction of these fungal structures in trypan blue was highly variable and ranged from pale blue to almost colourless. No vesicles were observed in any roots.

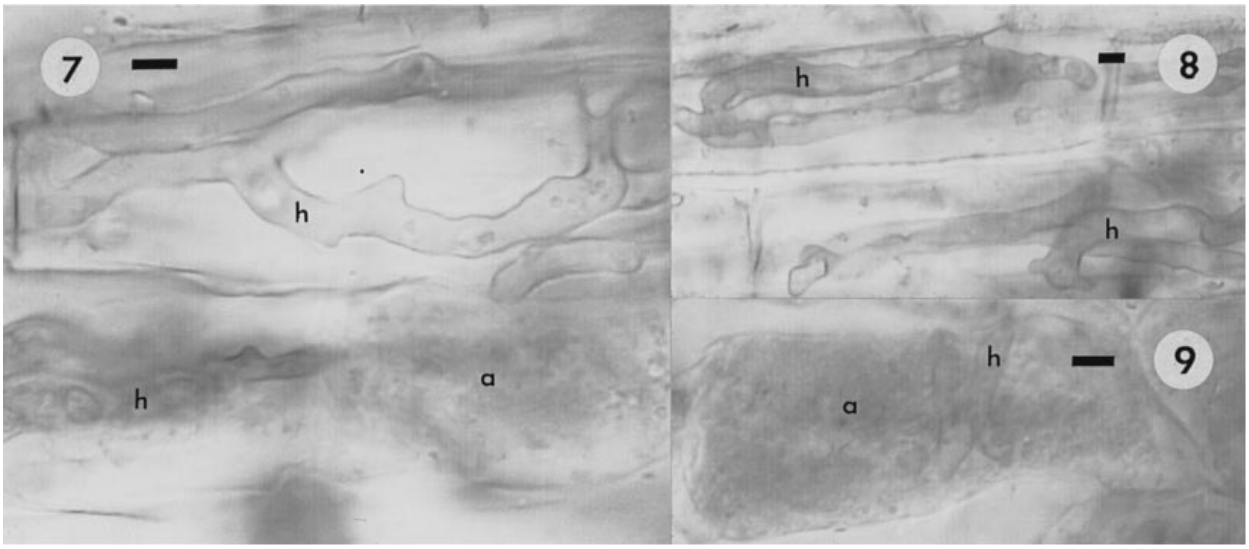
Specimens of A. appendicula *examined*. Colombia, native grasses and tropical kudzu near Carimagua, from CIAT culture C-13-1 (OSC 41,495, Holotype, FLAS F53673, Isotype); Brazil: near Araripina, Pernambuco, 24 Feb. 1995, L. Maia (INVAM BR229); Nicaragua: pasture soil, region unknown, 30 Aug. 1993, C. Picone (#02, INVAM NI105); Venezuela: grass-legume pasture near Guanare, 8 Oct. 1989, M. Carreno (INVAM VZ856); U.S.A.: University of Florida turf plots, Gainesville, Florida, A. E. Dudeck (INVAM FL130A); acid minesoil near Morgantown, West Virginia, associated with *Andropogon virginicus* L., 14 Apr. 1993, J. Morton (INVAM WV109C); old field in Durham, North Carolina, P. Schultz (#227, INVAM NC171), J. Bever (#220, INVAM NC169).

Specimens of A. gerdemannii *examined*. U.S.A.: Ona Florida, June 1978, N. C. Schenck (OSC 37,514, Holotype; FLAS F51804, Isotype); University turfgrass plots, Kingston, Rhode Island, April 1990, R. Koske (#3630).

Synanamorph

Glomus leptotichum N. C. Schenck & G. S. Sm. Mycologia **74**, 82–83. (1982).
= *Glomus fecundisporum* N. C. Schenck & G. S. Sm. Mycologia 74, 81–82. (1982).

We conclude that *Glomus leptotichum* and *G. fecundisporum* are conspecific, based on correspondence of spore morphology in type specimens and spores and vouchers from living cultures. With the same data of publication (Schenck & Smith, 1982), the name *G. leptotichum* is given priority for two reasons: (i) spores in type specimens were not as heavily parasitized as those in the types of *G. fecundisporum* and (ii) voucher specimens exist of freshly extracted spores from INVAM reference accession FL184 identified by one author of the protologue (N. C. Schenck). Foreign hyphae are associated



Figs 7–9. Mycorrhizas of *Acaulospora gerdemannii* and *Glomus leptotichum* **Fig. 7.** Coiled and knobby hypha (h) and degrading arbuscule (a) of INVAM accession NC169 in 30-day-old maize root cells stained in trypan blue. This culture produced spores of both synanamorphs, slide # 2988, bar = 5 μm. **Fig. 8.** Coiled hyphae (h) within 30-day-old maize root cells colonized by INVAM accession FL184 and stained with trypan blue. Only *G. leptotichum* sporulated in this culture, slide # 2986, bar = 5 μm. **Fig. 9.** An arbuscule (a) with a cortical cell of the same maize root, bar = 5 μm.

with many of the spores in the holotype of *G. fecundisporum*, which suggests that parasitism may have been an important factor affecting morphological features and leading the authors to consider it a distinct species. The protologue also supports this conclusion, since spores are described as varying in colour from white to black. Such a colour range is unknown as a heritable trait in any other species of Glomales (Morton, 1988), but can occur in cultures of many light-spored *Glomus* spp., such as *G. leptotichum*, from parasitism or degradation during prolonged storage (Morton, unpublished).

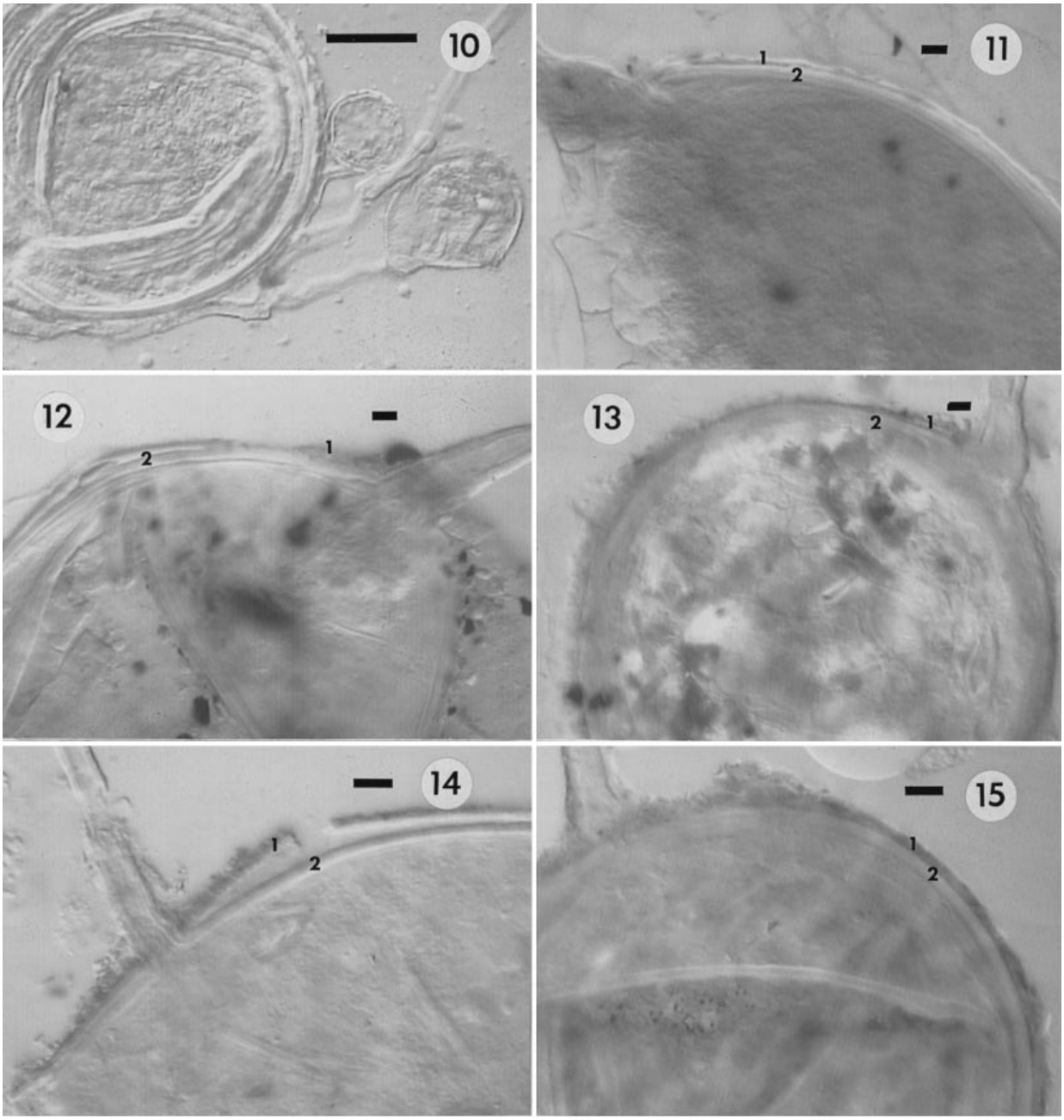
Spores are formed blastically on the terminal ends of hyphae in soil. In all INVAM cultures of *G. leptotichum*, either sporulating alone or with *A. gerdemannii* (Fig. 1), subtending hyphae branched and bore smaller (35–50 μm) and thinner-walled 'vesicles' (Fig. 9) as described for the *Glomus* morphotype in the protologue of *A. appendicula*. Wall structure of these vesicles is similar to that of larger spores except that they are thinner. Developmentally, this small difference can be attributed to progenesis, a heterochronic event in which spore wall differentiation terminates early, together with cessation of spore expansion. Small spores of similar size range also were present in type specimens of *G. fecundisporum*, but they were poorly preserved (or degraded from parasitism).

Spores of *G. leptotichum* and *G. fecundisporum* are both described as being globose to irregularly shaped, the former 48–262 μm and the latter 60–270 μm diam. Spores from the INVAM reference culture of *G. leptotichum* (FL184) showed similar variation in shape. Spores in different INVAM cultures synonymized with *G. leptotichum* are 60–250 μm diam., which overlaps that reported in both protologues.

Freshly-extracted and healthy spores from all cultures of *G. leptotichum* are white to cream-coloured (0–0–15–0). This colour range corresponded only to that described in the protologue of *G. leptotichum*, Spores of *G. fecundisporum* were reported by Schenck & Smith (1982) as being of a similar colour range in youth and then darkening to brown to black at maturity. We consider this description to be an artifact of spore parasitism and thus is not taxonomically informative.

The subcellular structure of *G. fecundisporum* spores is described as consisting of two separable walls of equivalent thickness and no reticulum on the outer wall. Spores of holotype and isotype specimens often showed evidence of only one wall. When two were present, the outer one was thin (Fig. 10). Spores of *G. leptotichum* are reported as having only one wall with an 'indistinct alveolate reticulum of shallow ridges'. However, spores in type specimens of *G. leptotichum* and *A. appendicula* possessed a wall structure identical to that described for *G. fecundisporum* (Figs 11–12) except that the outer wall was thicker and more persistent. Freshly extracted spores of *G. leptotichum* from INVAM cultures showed two robust walls (Figs 13–14). The outer one is cream (0–0–15–0) to pale yellow-brown (0–10–20–0), loosely organized, and 4–20 μm thick (depending on degree of degradation or sloughing) (Fig. 13). It appears to attract debris with age. This wall produces a pale to dark reddish-brown reaction in Melzer's reagent (Fig. 14) identical to that described for the *Glomus* morph in the protologue of *A. appendicula*. The second wall fits the definition of a 'laminate wall' (Walker, 1983), except that the laminae are semi-flexible, tend to be resilient and fold when pressure is applied in slide mountants (Figs 10–14). This folding can create the appearance of thin flexible inner walls, but no evidence of their presence could be confirmed. The laminate wall is hyaline to pale yellow (0–0–10–0) and 4–5 μm in thickness.

The width of extramatrical hyphae of *G. leptotichum* cultures spans that reported for the species (8–18 μm) and *G. fecundisporum* (12–22 μm). Hyphal wall structure was indistinguishable, consisting of one layer continuous with the laminate wall of the spore and remnants of the spore outer wall (Figs 9–14).



Figs 10–15. *Glomus leptotichum* **Fig. 10.** Hypha with large spore and two smaller spores described as 'vesicles' by Schenck *et al.* (1984), from INVAM accession FL184; bar = 50 µm. **Fig. 11.** Broken spore from a slide of the holotype of *G. fecundisporum* (OSC 40,250), showing a thin outer wall (1) and thicker 'laminate wall' (2); bar = 10 µm. **Fig. 12.** Broken spore from a slide of the holotype of *G. leptotichum* (OSC 40,249), showing two walls of near-equal thickness (1–2); bar = 10 µm. **Fig. 13.** Broken spore from a slide of the isotype of *A. appendicula* (FLAS F53,673), showing both walls and the plasticity of wall 2 after crushing; bar = 10 µm. **Fig. 14.** Broken spore freshly extracted from INVAM accession FL184 and mounted in PVLG, with both walls clearly visible and continuing into the subtending hypha (arrow); slide #1881; bar = 10 µm. **Fig. 15.** Broken spore freshly extracted from INVAM accession FL184 and mounted in PVLG + Melzer's reagent, showing the differential red-brown reaction of wall 1; slide #2990; bar = 10 µm.

Mycorrhizas of *G. leptotichum* and *G. fecundisporum* are described similarly as staining so faintly in trypan blue that only hyphae in outer cortical cells are visible. That observed in 30-day-old corn roots formed by the fungus INVAM accession FL184 (yielding only *G. leptotichum* spores) also formed many pale-staining hyphae and arbuscules (Figs 8–9). However, some hyphae and arbuscules stained more darkly and were readily discernible throughout the root cortex. The mycorrhizas were indistinguishable from those of accession NC169. No experiments were carried out to determine if the absence of vesicles was a heritable trait or a response to environmental variables.

Specimens of G. leptotichum *examined.* U.S.A.: Live Oak, Florida, bahia grass pot culture of maize roots, May 1981, N. C. Schenck (OSC 40,429, Holotype; FLAS F52577, Isotype); location unknown, N. C. Schenck #184 (INVAM FL184); University turfgrass plots, Gainesville, Florida, A. E. Dudeck (INVAM FL130A); University turfgrass plots, Kingston, Rhode Island, April 1990, R. Koske

(#3630, #3636, #3438); acidic minesoil near Morgantown, West Virginia, associated with *Andropogon virginicus* L., 14 Apr. 1993, J. Morton (INVAM WV109C); old field in Durham, North Carolina, P. Schultz (#227, INVAM NC171), J. Bever (#220, INVAM NC169); Brazil: near Araripina, Pernambuco, 24 Feb. 1995, L. Maia (INVAM BR229); Mexico: 7 Oct. 1992, L. Varela (INVAM MX982A); Nicaragua, pasture soil at unknown location, 30 Aug. 1993, C. Picone (#02, INVAM NI105); Nigeria: near Sadore, D. Wetterlein (INVAM NG107C); Venezuela: grass-legume pasture near Guanare, 8 Oct. 1989, M. Carreno (INVAM VZ856).

Specimens of G. fecundisporum *examined*. U.S.A.: University Agronomy Farm soybean plots, Gainesville, Florida, May 1981, G. M. Chaves (OSC 40,250, Holotype).

The occurrence of two synanamorphs in separate families of Glomales is unusual. It may be a result of the unique evolutionary history of this group (Morton, 1990). However, it is more likely that one of the two synanamorphs has been grouped incorrectly because of misinterpretation of morphological characters that were defined phenetically until recently (Morton, 1993). Comparative developmental studies are underway to redefine these characters (Morton *et al*., 1995) and to reinterpret phylogenetic relationships of both synanamorphs that will determine if one or the other should be transferred to Glomaceae or Acaulosporaceae.

We thank Bill Wheeler, Anne Zondlo, and Steve Bentivenga for assistance in carrying out greenhouse experiments; Drs Aaron Liston and Richard Halse at Oregon State University and Drs Gerald Benny and James Kimbrough at University of Florida for providing holotype and isotype specimens, respectively; Dr Rick Koske and an unnamed reviewer for helpful editorial comments. This work was supported by Hatch Funds from the West Virginia Agricultural and Forestry Experiment Station and National Science Foundation grant BIR-9015519 to J.B.M.

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(*Accepted 10 October 1996*)