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The Australian zygomycetous mycorrhizal fungi. II. Further Australian sporocarpic Glomaceae

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Abstract. *Glomus atrouva*, *G. canum*, *G. cuneatum* and *G. pellucidum* sp. nov. are described from eastern New South Wales. New distributional data and redescrptions are presented for *G. australe*, *G. fuegianum*, *G. fulvum* and *G. pubescens*, the last three being first reports for Australia. New records of *G. caledonium*, *G. macrocarpum* and *G. tenerum* are also included.

Introduction

Zygomycetous mycorrhizal fungi are important in the nutrition and physiology of their photosynthetic partner (Smith and Read 1997) and aid macroaggregation of soil particles (Tisdall 1991). Sporocarpic species are a component of the diet of some small animals (McGee and Baczocha 1994; Claridge *et al.* 1996). The phylogenetic relationships within this functional group are unclear (Morton *et al.* 1995). Morton and Benny (1990) argue for its placement into two orders, Glomales for arbuscular mycorrhizal species that form blastospores and Endogonales for ectomycorrhizal or saprobic species that form zygospores. A further group contains ectomycorrhizal fungi that form sporocarps of blastospores (McGee 1996).

The genus *Glomus* in the Glomaceae includes many species that form sporocarps. Sporocarps range from relatively simple to complex structures. The simplest are single blastospores surrounded by a weft of hyphae, such as *Glomus monosporum* Gerdemann & Trappe. In the most complex, spores are contained within a differentiated hyphal network and the sporocarp has a predictable morphology, including a peridium, such as *Glomus warcupii* McGee, a hollow central core, such as *Glomus cerebriforme* McGee, or many clusters of spores arising from a modified hypha called a centrum, such as *Glomus australe* (Berkeley) S.E.Berch. In this paper, the words 'cluster' or 'aggregate' refer to a secondary arrangement of spores within a sporocarp (Berch and Fortin 1983). Members of the genus may also form spores singly in soil or roots. Many species that form spores in sporocarps may also form them singly in soil, e.g. *Glomus*

mosseae (Nicolson & Gerdemann) Gerdemann & Trappe. Others are not known to form single spores outside the tissue of the sporocarp, such as *Glomus tenerum* Tandy emend. McGee. A continuum of form from single spores to sporocarps is found within the genus.

Sporocarpic members of Glomaceae commonly occur in and on largely undisturbed soils (Tandy 1975; McGee 1986). We are investigating their use in the revegetation of highly disturbed habitats to encourage survival of the native vegetation and return of small mammals. Several collectors have provided collections from around Australia for our examination. In this paper, we describe some new species, redescribe some poorly understood species, report first records of some species for Australia and extend information on our understanding of their biology and distribution.

When spores are not globose, their sizes in the descriptions are given with the diameter along the axis of the hyphal attachment first and at right angles to the hyphal attachment second.

Herbarium abbreviations of collections cited are DAR (Orange Agricultural Institute), H (CSIRO Forestry and Forest Products, Wembley, WA) and MEL (National Herbarium of Victoria, Melbourne).

Descriptions of new species

1. *Glomus atrouva* McGee & Pattinson, sp. nov.

Sporocarpia firma, rotundata, usque ad 1 cm lata, soli, fragmentorum radicellum, hypharum et sporarum

composita. Peridium absens. Fasciculi uvoidei usque ad 30 sporarum atrobrunnearum per sporocarpium dispersi et in pagina manifesti. Sporae unusquisque fasciculi in plexus hypharum anastomosentium orientes. Sporae globosae vel subglobosae, versus hypham affixam leviter decrescentes, $100 \times 100\text{--}180 \times 200 \mu\text{m}$, parietibus duobus: paries exterius fragilis, brunneus, $4\text{--}10 \mu\text{m}$ crassus; paries interius secedens, brunneus, lamellatus, $10\text{--}20 \mu\text{m}$ crassus. Hypha subtenta $18\text{--}25 \mu\text{m}$ lata, ad sporam angulam 90° affixa. Holotypus G. Pattinson, NH1.10 (DAR 74519).

Sporocarps firm, rounded, up to 1 cm broad, composed of soil, root fragments, hyphae and spores, lacking a peridium. *Gleba* with grape-like clusters of up to 30 dark-coloured spores dispersed throughout and apparent at the surface.

Spores arising blastically from hyphal loops within a plexus of anastomosing hyphae (Fig. 1A), globose to subglobose, tapering slightly towards the attached hypha, $100 \times 100\text{--}180 \times 200 \mu\text{m}$ with two walls: outer wall brittle when mature (Fig. 1B), brown, $4\text{--}10 \mu\text{m}$ thick: inner wall separable, laminated, brown, $10\text{--}20 \mu\text{m}$ thick, thickest at spore base. Contents of the spore are cut off by expansion of the inner wall at the base of mature spores. Subtending hypha $10\text{--}80 \times 18\text{--}25 \mu\text{m}$, sometimes slightly constricted at the point of attachment when immature, attached at right angles to the spores, the two spore walls continuing down the subtending hyphae: outer wall $1\text{--}3 \mu\text{m}$ thick, initially hyaline and laminated, by maturity brown and brittle; inner wall initially hyaline and membranous, by maturity brown, laminate and $3\text{--}8 \mu\text{m}$ thick.

Gleba with hyphae $4\text{--}6 \mu\text{m}$ broad.

Etymology

Latin, *atro-* (dark) and *uva* (grape), referring to the dark spore clusters that appear at the surface of the sporocarp like grape clusters. As a noun serving as the epithet, *atrouva* retains its feminine ending.

Distribution, habitat and season

Only known from New South Wales, central coast and from pot cultures started with spores from those localities; summer and autumn.

Collections examined

Holotype—NEW SOUTH WALES: Sydney, North Head Quarantine Station, from a pot culture originating from spores in scats of rats, *Rattus* sp. found at that locality, *G. Pattinson* NH 1.10, 30.v.94 (DAR 74519). Paratypes—NEW SOUTH WALES: Sydney, North Head, from a pot culture originating from spores in scats of *Rattus* sp. found at that locality, *G. Pattinson* NH 1.4 & NH 1.8, 30.v.94 (DAR 74523 & 74524). Morristet, Eraring Scientific Reserve in scat of bandicoots, *Perameles nasuta*, *M. Odewahn*, EScO1, 10.ii.2000 (DAR 74943). Pearl Beach, Crommelin Research Station, in scat of *Rattus fuscipes*, *P. McGee*, WScM6, 26.iii.2000 (DAR 74942).

Remarks

Before spore formation, the inner wall of the sporogenous hypha is membranous. As the wall thickens, the inner wall darkens. The outer wall is initially laminated and hyaline to pale brown and as it darkens, it also becomes brittle. Spores form after a hyphal bud in the plexus elongates and the apex expands. During elongation of hyphae and particularly during formation of blastospores, the inner wall of the subtending hypha thickens and continues thickening after the spore has reached its mature size.

In arbuscular mycorrhizas, hyphae are initially $2\text{--}3 \mu\text{m}$, with the outer wall thicker than the inner. With maturation of the fungus in the colony, diameters of the hyphae increase and their inner wall thickens. Arbuscular mycorrhizas typical of *Glomus* species are formed. Spores are also formed soon after initiation of mycorrhizas. Shape of intraradical spores varies with host, although they are usually ovoid and $90\text{--}180 \times 70\text{--}90 \mu\text{m}$. Rarely, spores are densely packed in parts of colonised roots.

Glomus atrouva resembles *G. australe* and *G. macrocarpum* Tulasne & C. Tulasne: these three form sporocarps containing 2-walled spores and the spore hyphal attachment remains open until maturity. In *G. australe*, spores are formed in clusters primarily from lateral and terminal projections of a hypha arising from a centrum. The outer spore wall is hyaline to pale yellow and not brittle. A septum may close off the contents of the spore. In *G. macrocarpum*, spores are formed randomly through the sporocarp, not in aggregates or clusters. The spore is also lighter in colour than *G. atrouva*, the outer wall being hyaline and the inner wall yellow to pale brown. Spores of *G. atrouva* arise from a plexus of anastomosing hyphae and follow a different development pathway than the other two species and both walls of spores and hyphae are darker at maturity.

Glomus atrouva has been collected from scats of small mammals (McGee and Baczocha 1994) from coastal sandy soils of central New South Wales. Extracted spores have established and maintained in pot culture through several transfers (Pattinson *et al.* 1999). Sporocarps form in pot culture from 6 weeks onwards, depending on the amount of inoculum. Spores from scats are similar to those from pot cultures and many sporocarps incorporate fresh root material, suggesting the mammals collect the fungi from below ground.

2. *Glomus canum* McGee, sp. nov.

Sporocarpia mollia, rotundata, usque ad 2 mm lata; peridio cano, byssaceo, hypharum collapsarum $2\text{--}5 \mu\text{m}$ latorum composita, interne massa brunnea sporarum hypharumque, ad paginam soli per funiculum hypharum appressarum affixa. Sporae globosae vel subglobosae, $30\text{--}50 \mu\text{m}$ latae, cum pariete uno lamelloso, luteo vel pallide brunneo, $2\text{--}10 \mu\text{m}$ crasso, guttulae tenues hyalinae continentia. Hyphae

glebae 2–5 µm latae, amorphae, plerumque collapsae. Hyphae subtentae 3–4 µm latae, parietibus tenuibus luteolis, ad sporam angulam 90° affixa, a contentis sporae septo separata. Holotypus: P.A. McGee (DAR 69425).

Sporocarps soft, rounded, up to 2 mm broad, attached to the soil surface by strands of appressed hyphae, with a white cottony peridium of collapsed, hyaline, thin-walled hyphae 2–5 µm broad. *Gleba* a brown mass of spores and hyphae.

Spores globose to subglobose, 30–50 µm broad, with a single laminate yellow to pale brown wall 2–10 µm thick, containing fine hyaline oil droplets (Fig. 1C). *Subtending hypha* 3–4 µm broad, with thin yellowish walls, attached at right angles to the spores and separated from the spore contents by a septum.

Gleba of thin-walled, pallid hyphae 2–5 µm broad, usually collapsed and amorphous.

Etymology

Latin, *canum* (white haired), in reference to the appearance of the peridium.

Distribution, habitat and season

Known only from the type locality in New South Wales, Styx River State Forest, under rubble on a steep slope in rainforest; September.

Collections examined

Holotype—NEW SOUTH WALES: Styx River State Forest, P. A. McGee SM15, 28.ix.89 (DAR 69425). Paratype—NEW SOUTH WALES: Styx River State Forest, P. A. McGee SM16, 28.ix.89 (DAR 69426).

Remarks

Walls of spores of *G. canum* expand rapidly when mounted in acidic (such as lactic acid) or basic (such as ammoniacal Congo red) mountants including PVA lactoglycerol (Omar *et al.* 1979). In water, the walls differ from those of the genus *Densospora* (McGee 1996), lacking the infrequent spores where the lumen is almost entirely filled with wall material. Reaction to various stains including Melzer's reagent was inconsistent.

Glomus canum is close to *G. microcarpum* Tulasne & C.Tulasne, *G. pallidum* Hall and *G. pulvinatum* (P.Hennings) Trappe & Gerdemann (table 1, McGee 1986). It differs from *G. microcarpum* in having a cottony peridium, collapsed glebal and peridial hyphae and a septum separating spore contents from the subtending hyphae. *Glomus pallidum* has hyaline spore walls, occasional septa in the subtending hyphae and a poorly developed peridium. *Glomus pulvinatum* has larger spores, hyaline spore walls and much broader subtending hyphae. *Glomus nanolumen* Koske & Gemma also forms spores in sporocarps, but these lack a peridium and their spores have massively thickened walls.

The mycorrhizal relations of *G. canum* are unknown. No potentially ectomycorrhizal hosts were near the collection site.

3. *Glomus cuneatum* McGee & Cooper, sp. nov.

Sporocarpia firma, rotundata, 2–12 mm lata, undulatis inaequalibus et pyramidalibus, stipite usque ad 3 mm latis. Peridium album, hyphis 1.5–4 µm latis. Gleba maturitate segmentis cuneatis lateraliter formatis in collocacione flabellate. Sporocarpia secta liquidum luteum viscosum producentia. Sporae in segmentis cuneatis glebae inclusae, globosae, ovoideae, clavatae vel irregulares, 70–70–120 × 180 µm diametris maximis, pariete singulari, bicolorato, laminari, 8–12 µm crasso; lamina exterior nigra, 3–6 µm crassa. Hypha subtenta 8–12 µm lata, ad sporam angulam 90° affixa. Holotypus: A. Cooper (DAR 74519).

Sporocarps firm, rounded, 2–12 mm broad, with uneven, superficial pyramidal undulations that are the apices of cuneate segments that form laterally in sporocarps as they mature, attached to soil by a stipe up to 3 mm thick and giving the appearance of a tiny basidiocarp in vertical cross-section (Fig. 1D). *Peridium* white, of thin-walled hyphae 1.5–4 µm broad, extending down the surfaces of each cuneate segment. *Gleba* with black spores embedded firmly amongst hyphae of cuneate segments, the most mature spores concentrated towards the outer radial surface of a segment and arranged with the attached hyphae aligned towards the stipe; spores absent from stipe; some soil fragments embedded between though not within cuneate segments; a yellow viscid fluid released from parts eaten by insects or when the fresh sporocarp is sectioned (Fig. 1D).

Spores globose to ovoid, clavate or irregular, 70 × 70–120 × 180 µm, the longer dimension of the elongate spores either along or across the spore axis, with a single laminated wall 8–12 µm thick, the outer 3–6 µm of the wall black and overlying a hyaline inner zone (Fig. 1E), initially pale brown and budding from the terminus of a pale brown, sporogenous hypha, which subsequently produces additional spore-bearing branches below the initial terminal spore, these branches often forming secondary, spore-bearing branches; spore contents separated from subtending hypha by wall-thickening. *Subtending hypha* attached at right angles to the spore and separated from the spore contents by wall-thickening, 15–24 µm broad at the spore wall, thinning to less than 10 µm within 50 µm of the spore, composed of a single wall less than 6 µm thick at the connection with the spore, pale brown at the surface, becoming hyaline and less than 1 µm thick within 50 µm of the spore.

Gleba of hyaline hyphae continuous with the peridial hyphae, 1.5–8 µm broad, with walls up to 1 µm thick.

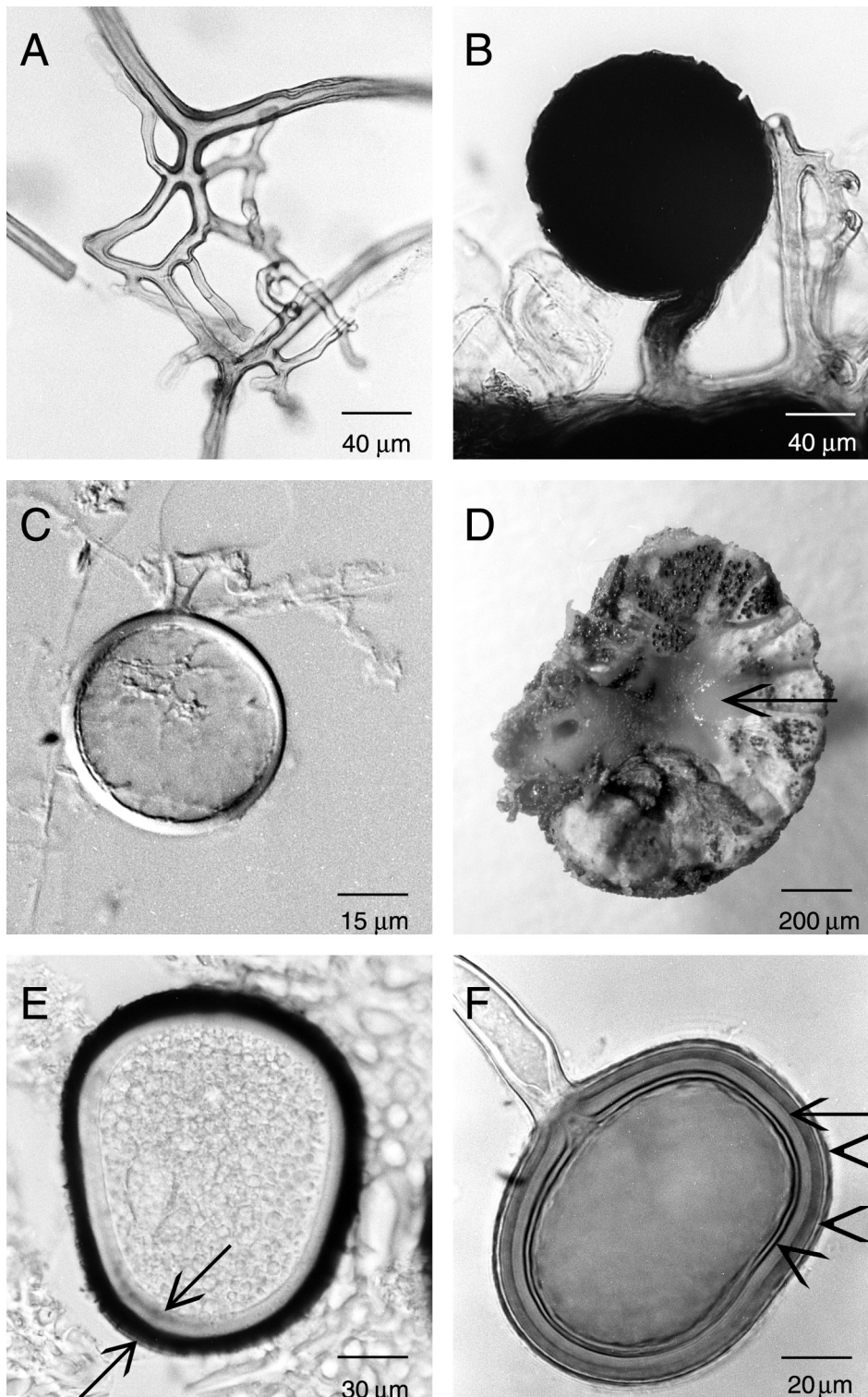


Fig. 1. (A) *Glomus atrouva* (DAR 74519): an anastomosing plexus of hyphae from which spores arise. (B) Mature spore of *Glomus atrouva* (DAR 74519) showing cracks in the brittle outer wall. (C) Spore of *Glomus canum* (DAR 69425). (D) Face of a vertical section cut through a sporocarp of *Glomus cuneatum* showing stipe and segments wedged together. The mucilage that is apparent between segments and especially in the core of the stipe after sectioning is arrowed. (E) Section through the wall of a spore of *Glomus cuneatum* showing the distinct deposit of dark material in the outer zone. The inner and outer face of the wall are arrowed. (F) Spore of *Glomus pellucidum* (DAR 74552) showing three walls (arrow heads), with the middle wall having separated into two laminations (arrow pointing to the zone of separation).

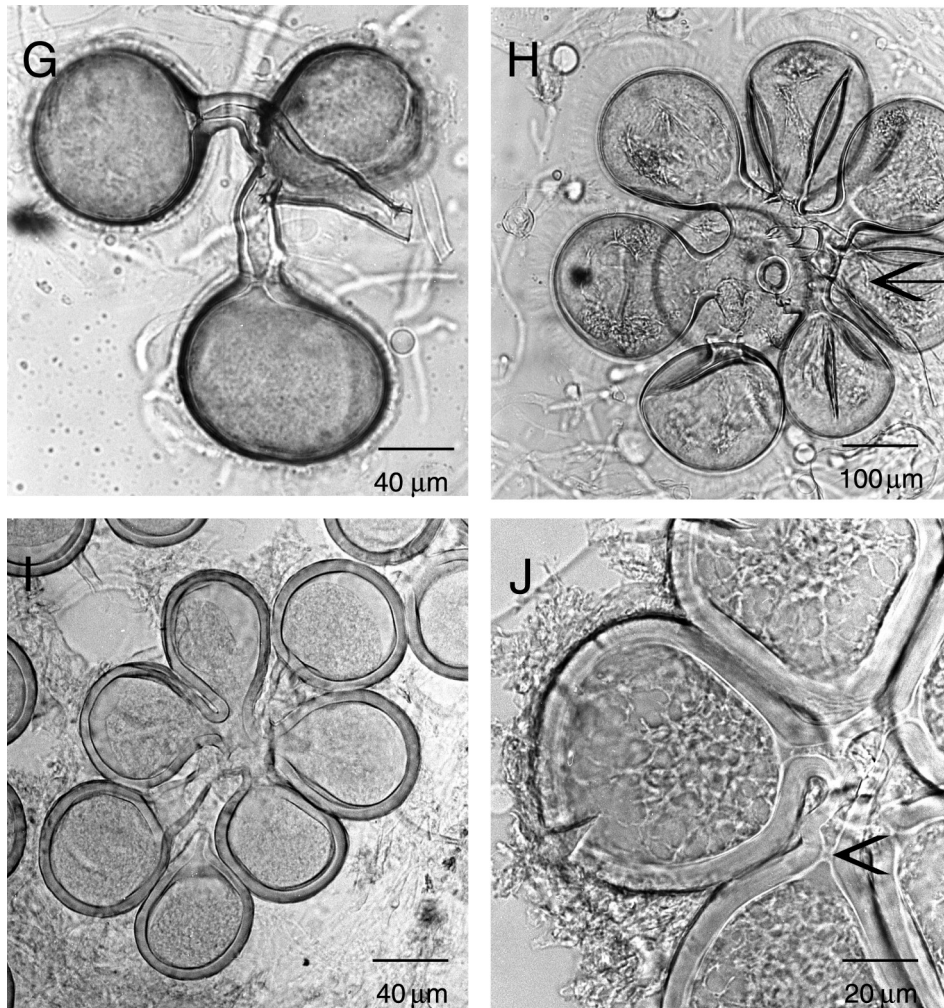


Fig. 1. (continued) (G) An immature cluster of spores of *Glomus australe*. The isolate is of the small-spored form with pores closed by septa. (H) Spores of *Glomus australe* arising from a thin-walled centrum (arrow). The isolate has large spores and these remain open at maturity. Scale bar = 100 μm . (I) Cluster of spores of *Glomus fuegianum*. (J) *Glomus fuegianum* with yellow inner wall and hyaline outer wall. Arrowhead points to the pore closure.

Etymology

Latin, *cuneatum* (wedge-shaped) in reference to the cuneate segments of the sporocarp.

Distribution, habitat and season

Only known from eastern Australia, year round.

Collections examined

Holotype—NEW SOUTH WALES: Royal National Park at Audley Rd entrance, *Alex Cooper* NC1, 24.ii.95 (DAR 74520). Paratypes—NEW SOUTH WALES: Royal National Park at Audley Rd entrance, *Alex Cooper* NC3, 3.33.95 (DAR 74519) and NC14, 10.iv.95 (DAR 74521). QUEENSLAND: Mt Spec. Site 2, *T. Grove*, 10.iv.1989 (H4412).

Remarks

Spores of *Glomus cuneatum* first develop blastically from a hyphal terminus. Several spores may subsequently arise from

the same sporogenous hypha, emerging below the terminus in a determinate manner. The wall of the hypha and spore initial is pale brown and initially <1 μm thick. Only spores and sporogenous hyphae are brown. As a spore expands, wall material is laid down on the inside. It is unclear when hyaline material is laid down, but it commences prior to complete expansion of the spore.

Spores are difficult to remove from sporocarp segments, although the segments separate readily from each other. Even segments that have been chewed by arthropods are firm and difficult to tease apart. Spores usually become apparent only when the hyphae are teased from the segments. In transmission electron microscopy (TEM), adhesion between hyphae and spores is suggested by the presence of a continuous matrix. The spores are extremely difficult to squash and sections cut through either sporocarps or segments suggest two walls of

different colour (Fig. 1E). On microscopic examination it is evident that the wall is uniformly laminated and colour is deposited mostly in the outer zone.

Glomus cuneatum is distinct from all other described species of *Glomus*. *Glomus segmentatum* Trappe, Spooner & Ivory also has a segmented sporocarp, but its spores are smaller than those of *G. cuneatum* and have two thin, hyaline walls. The colour deposits in the walls of spores of *Glomus melanosporum* Gerdemann & Trappe are similar to those of *G. cuneatum*. However, the former has larger spores and its sporocarp is not segmented. In addition, some scats from rats contain cuneate segments with spores that are consistently smaller. These spores have not initiated mycorrhizas (see below) and the sporocarp from which they were removed is unknown. The presence of yellow exudate, a brown–black–coloured deposit in the outer but not inner zone of the single spore wall and very fine hyphae surrounding and adhering to the spores differentiate *G. cuneatum* from all known species with similarly sized spores.

Glomus cuneatum occurs widely within eastern New South Wales within scats of *Rattus* and *Perameles* spp. throughout the year (McGee and Baczocho 1994; P. A. McGee, unpubl. data) and as fresh sporocarps in autumn and winter. Fresh sporocarps are attractive to arthropods, which graze on the peridium, thereby exposing black spores.

The mycorrhizal status of *Glomus cuneatum* remains unknown. Numerous attempts to produce mycorrhizas by inoculating freshly collected spores in autoclaved soil under *Allium*, *Trifolium*, *Acacia*, *Leptospermum*, *Melaleuca* and *Eucalyptus* spp. have failed. On one occasion, fine hyphae were observed attached to the root surface of *Melaleuca uncinata*, but the fungus failed to transfer following further inoculation on seedling roots. Attempts to culture the fungus on potato dextrose agar, nutrient dextrose agar (full strength and 1/10 strength) and malt marmite agar have also failed. The fungus may not form mycorrhizas, but fresh sporocarps have always been collected only from under hosts that form ecto- and arbuscular mycorrhizas.

4. *Glomus pellucidum* McGee & Pattinson, sp. nov.

Sporocarpia hypogaea, rotundata vel irregularia, solum et radicellas includentia, usque ad 2 cm lata. Sporae in aqua pellucidae, globosae vel subglobosae, 60–110 µm diametris vel obovatae et 130 × 50 µm, parietibus complexis: stratum externum 0.5–1 µm crassum, juventute mucilaginum, maturitate interdum evanescens; stratum medium luteum vel glandulaceum, 8–12 µm crassum, in nonnullis sporis in strata duo, unterque 4–8 µm crassa, findens; stratum intimum hyalinum, membranaceum, usque ad 1 µm crassum, tantum in nonnullis sporis maturis inventum. Hypha subtenta 11–14 µm lata. Holotypus: G. Pattinson (DAR 74552)

Sporocarps hypogeous, rounded to irregular, enclosing soil and roots, up to 2 cm in diameter lacking a peridium.

Spores globose to subglobose 60–110 µm in diameter or occasionally obovate and up to 130 × 50 µm, arising blastically mostly in a racemose or occasionally flabellate arrangement on sporogenous hyphae woven together in clusters so that spore initials appear to arise from a plexus of hyphae; wall structure complex: outer wall hyaline, 0.5–1 µm thick, mucilaginous when immature, becoming flaky and often lost at maturity; middle wall yellow to yellow brown, laminate, in some spores splitting into two separable walls, each 4–8 µm thick to total 8–12 µm when mature; inner wall present only in some mature spores, hyaline, membranous, up to 1 µm thick (Fig. 1F). *Subtending hypha* 11–14 µm broad at the attachment, separated from the spore contents by a plug or thickening of the inner wall in mature spores, all spore walls continuing down the subtending hyphae and aggregating 6 µm in thickness at the attachment, thinning to 2 µm within 50 µm of the spore.

Gleba of hyphae 11–14 µm broad with at least two walls each c. 1–3 µm thick.

Etymology

Latin, *pellucidum* (translucent), referring to the translucence of spores on the surface of sporocarps when immersed in water.

Distribution, habitat and season

Known only from the Sydney Basin, New South Wales; year-round.

Collections examined

Holotype—NEW SOUTH WALES: Sydney, North Head, from a pot culture originating from spores in scats of *Rattus* sp. found at that locality, *G. Pattinson* NH 1, 5.v.1994 (DAR 74552). Paratypes—NEW SOUTH WALES: Sydney, North Head, from a pot culture originating from spores in scats of *Rattus* sp. found at that locality, *G. Pattinson* NH 1.7, 30.v.1994 (DAR).

Remarks

Spores develop by initial expansion of a lateral bud from within a complex of hyphae. The initial two walls expand, the outer being thin and ephemeral and sometimes lost as the spore ages. The inner wall expands once a spore has reached its mature diameter and may split into two distinct walls. The split does not necessarily occur evenly. Once the spore is mature, a third hyaline membranous wall forms within it and the attached hypha and a plug develops to block the spore if the walls have not already closed the pore. Despite the formation of spores from a central plexus of hyphae, spores appear to be distributed randomly throughout the sporocarp.

Mycorrhizas formed by this fungus have vesicles 70–100 µm long by 50–75 µm wide and intraradical hyphae 2–7 µm in diameter with at least two walls. The laminated

wall thickens with age and the lumen of hyphae may become occluded.

The extraradical phase also differentiates this fungus. In pot culture, the runner hyphae addressed to root surfaces release mucilage that appears to be associated with adhesion to the surface of the root.

Few glomalean fungi form spores with three walls. Of these, the spores of *Glomus geosporum* (Nicolson & Gerdemann) Walker are larger overall, have a greater range of sizes and the mid-wall is darker than for *G. pellucidum*. Spores of *Glomus maculosum* Miller & Walker are larger than those of *G. pellucidum* and characterised by ingrowths of the inner wall. Ingrowths have never been found in *G. pellucidum*. Sporocarps are unknown for *G. maculosum*.

The pot cultures on which this fungus is described originated from spores collected from scats recovered from faeces of *Rattus* and *Perameles* spp. trapped at North Head, Sydney, New South Wales, Australia (McGee and Baczocha 1994). The fungus has been extracted from scats collected subsequently from Kurringai Chase National Park (E. Sutherland, G. S. Pattinson and P. A. McGee, unpubl. data). We have not collected sporocarps of the fungus directly from soil, although the lack of sand in fragments from some scats suggest the sporocarps may form epigeously in the field.

New records and redescrptions

5. *Glomus australe* (Berk.) S.M.Berch & Fortin

Sporocarps up to 15 × 12 mm, rounded, with a white to pale yellow, cottony peridium and containing occasional soil and plant fragments. Surface and glebal hyphae white to cream colour.

Spores arising blastically in clusters that include mature and immature spores from a coarse terminal hypha which we term a centrum (Figs 1*G*, *H*), globose to subglobose, 160–300 µm in diameter in most Australian collections, 90–160 µm in a few collections, those near the sporocarp surface with relatively thin walls. Subtending hyphal centrum 25–60 µm in diameter at the spore wall, commonly open but occasionally blocked by thickening of the inner wall layer or a plug. All spores, subtending hyphae and centrum with two walls (Figs 1*G*, *H*) as described by Berch and Fortin (1983), except that the outer wall is laminated and becomes flaky on the surface with maturity.

Distribution, habitat and season

Eastern Australia including Tasmania (see also Berch and Fortin 1983), from woodlands to rainforest and cool temperate climates to tropics, forming arbuscular mycorrhizas in a range of plants. Its spores have been recovered from scats of *Rattus* sp. in Royal National Park (McGee and Baczocha 1994) and elsewhere on the east coast of Australia (P. A. McGee, unpubl. data) February through to July.

Collections examined

NEW SOUTH WALES: Barrington House, *N. Bougher*, 27.iv.1992 (H5581). Blue Mountains National Park, Bowen Ck, *P. McGee*, 20.vii.1989 (DAR 74525). Dorrigo National Park, along road to Bellington, *N. Bougher*, 1.v.1992 (H5858). Royal National Park, *P. McGee*, 14.vi.1990 (DAR 69429). QUEENSLAND: D'Aguilar State Forest, summit Mt Glorius, *J. Trappe*, 4.v.1992 (H6018). Gunawarra Site 9, *N. Bougher*, 8.v.1991 (H4688). Kirrama Site 4, *M. Amaranthus* 28.iv.1990 (H4558) & *S. Joyce*, 9.v.1991 (H4723). 5 km west Mount Glorius, *J. Trappe* and *R. Schaefer*, 4.v.1992 (H5993). Mt Glorius Site 4, *M. Amaranthus*, 16.v.1988 (H4240) and Site 6, *M. Amaranthus*, 30.iv.1990 (H4608). Mt Spec. Site 3, *T. Grove*, 10.iv.1989 (H4419). TASMANIA: Cave Rd, *C. Palzer*, 27.vi.1980 (DAR 69428). Base of Mt Wellington, *M. Castellano*, 17.v.1991 (H5358). Blue Gum Saddle, *N. Bougher*, 7.v.1990 (H1561). Ferntree, Mt Wellington, *C. Palzer*, 21.ii.1981 (DAR 69427). Lone Star Plantation, *R. Young*, 3.v.1990 (H1391). South of Golden Valley, *M. Amaranthus*, 5.v.1990 (H1512). West of Maydena, Styx Rd, *M. Castellano*, 16.v.1991 (H5167).

Remarks

Since Berch and Fortin (1983) redescribed *Glomus australe*, we have examined spore development in many sporocarps. Glebal hyphae initiate one, or rarely two, globose spores apically in immature sporocarps. Spores expand blastically and further spores are initiated from the terminus of the centrum or from lateral projections of the subtending hyphae. Walls of the spore, subtending hypha and centrum thicken and darken with maturity. Initially, the outer wall is flexible but becomes fractured and flaky as spores mature. The inner wall expands by the deposition of laminations on the inner side. Neither sporocarps nor single spores have formed in our pot cultures.

6. *Glomus caledonium* (Nicolson & Gerdemann) Gerdemann & Trappe

This species was originally described from spores sieved from soil. Sporocarps were subsequently described from North America (Gerdemann and Trappe 1974) and South Australia (McGee 1986). The collections cited below expand the known distribution of sporocarpic forms in Australia.

Distribution, habitat and season

Worldwide distribution, in Australia found in New South Wales, Queensland, South Australia, Tasmania and Western Australia, in forests. February through to July.

Collections examined

NEW SOUTH WALES: Coolumbooka Nature Reserve, AWC Site 150, *A. Claridge* 3103, 3.vi.1999 (DAR). QUEENSLAND: Atherton District, Mount Baldy, *J. Trappe*, 4.v.1988 (H4046) and *M. Castellano*, 3.ii.1992 (H5478). Kirrama Site 5, *M. Amaranthus*, 28.iv.1990 (H4569). Mt Glorius Site 4, *M. Amaranthus*, 16.v.1988 (H4233). TASMANIA: Blue Gum Saddle, *N. Malajczuk*, 7.v.1990 (H1570). Mt Field National Park Site 1, *B. Thomson*, 6.v.1990 (H1532), *R. Young*

and *M. Amaranthus*, 6.v.1990 (H1536) and *N. Malajczuk*, 6.v.1990 (H1540). South of Golden Valley, *J. Trappe*, 5.v.1990 (H1519). WESTERN AUSTRALIA: Boranup National Park, end of Point Rd, *J. Trappe* T14778, 20.vii.1993 (DAR)

Remarks

These collections resemble those from South Australia (McGee 1986), except that sporocarps are larger, up to 1 cm in diameter and the range of spore diameters greater, from 120 to 300 μm , in the most-extreme cases. Immature specimens can be easily confused with *G. australe*. The fungus forms spores blastically from hyphal terminals and in young sporocarps, the tangle of ballooning hyphal tips resembles immature sporocarps of *G. australe*. In mature specimens, the fungi are easily differentiated. Spores of *G. caledonium* arise from a tangled mycelium with no differentiation into clusters arising from a centrum. Sections of sporocarps have a solid mass of brown spores across the cut face.

7. *Glomus fuegianum* (Spegazzini) Trappe & Gerdemann

Sporocarps often attached to plant remains and connected to the soil with strands of white hyphae, white, rounded to flattened, up to 3 mm in diameter, cottony on the surface and with debris attached occasionally, usually without odour or latex when cut but some bruise easily when handled and then release cytoplasm into the glebal matrix and produce a white exudate when cut. Peridium 20–100 μm thick, of hyphae 1.5–4 μm in diameter. Clusters of 10–30 spores (Fig. 1I) dispersed through the sporocarp and readily separated from glebal hyphae. Immature spores usually occur near the sporocarp surface, although both mature and immature spores occur in most clusters. With maturity the spore clusters darken and glebal hyphae become less apparent at exposed surfaces.

Spores arising blastically from a centrum, globose to subglobose or broadly ovoid, often irregular in shape due to mutual pressure, 40–80 \times 45–80 μm , with hyaline contents and three unit walls (Fig. 1J)—external unit wall flaky, hyaline, usually less than 1 μm thick and indistinct, but sometimes up to 3 μm ; middle unit wall laminated, yellow, usually 4–6 μm thick; inner unit wall hyaline, less than 1 μm thick and apparent only in mature spores. Spore contents separated from subtending hypha at its narrowest point of attachment by what appears to be a plug of material similar to the inner wall, the plug seeming larger in spores from dried sporocarps.

Subtending centrum clavate, up to 40 \times 16–20 μm , tapering to 6–8 μm within 100 μm from the sporogenous zone of the centrum, the attachment with a lumen less than 2 μm broad for mature spores; centrum with three unit walls similar to those of spores, the walls aggregating 4–6 μm in thickness near the spore, thinning to less than 1 μm thick

within 100 μm from the sporogenous zone of the centrum. Glebal hyphae tend to be beaded, intricately interwoven, thin-walled, 4–6 μm in diameter.

Distribution, habitat and season

Apparently found worldwide, in Australia found in New South Wales and Tasmania, in forests and open scrub, under *Eucalyptus* spp., *Acacia dealbata* and *Tristania conferta*, forming arbuscular mycorrhizas in a range of plants; sporocarps have not formed in pot cultures (Pattinson, unpubl. data); February, March, May, August, September, December.

Collections examined

NEW SOUTH WALES: near Bilpin, *P. A. McGee*, 14.viii.1989 (DAR 69434) and 19.viii.1989 (DAR 69439). Royal National Park, *P. A. McGee*, 7.viii.1989 (DAR 69432, 69433), 1.xii.1998 (DAR 74532, 74533, 75434, 75435, 75436) and *A. Cooper* 24.ii.1995 (DAR 74527), 3.iii.1995 (DAR 74528), 23.iii.1995 (DAR 74529, 74530, 74531). TASMANIA: Hayes Rd, southern Tasmania, *C. Palzer*, 16.v.1985 (DAR 69437). Lisle, Bessell's Rd, *C. Palzer*, 25.ix.1981 (DAR 69436).

Remarks

These are the first reports of *Glomus fuegianum* from Australia, but the complex of fungi that form what we have called a centrum remains to be resolved. We first thought *G. fuegianum* to be a variant of *G. australe*. The two are similar in that spores arise in clusters from centra within the sporocarp. However, the spores of *G. fuegianum* are 40–80 μm in diameter, whereas the smallest spores of *G. australe* observed in our collections were 110 μm . Berch and Fortin (1983) reported that the nomenclatural type of *G. australe* has spores 120–180 μm in diameter (fig. 7), at the smaller end of the size range they observed in collections by L. Rodway from Tasmania. The outer unit wall of *G. fuegianum* is always hyaline and often difficult to discern. The outer wall of *G. australe* is hyaline to yellow, laminated and distinct, being 4–8 μm thick even in immature sporocarps. Spores of *G. fuegianum* and *G. australe* may be closed by a septum (Fig. 1G, J) but may remain open (Fig. 1H).

The Australian collections of *Glomus fuegianum* vary somewhat from those found in New Zealand (Hall 1977) and UK (Godfrey 1957; Yao *et al.* 1992). The group needs to be examined closely; differences appear in the peridial arrangement of the sporocarp, the wall number, the wall thickness and the colour and appearance of spores and sporocarps. The peridia of Australian sporocarps are cottony and pale-coloured. British collections mostly lack a peridium (Yao *et al.* 1992). Thaxter (1922) described reddish-brown spores with a single wall in *G. fuegianum*. The spore colour of the Australian collections is yellow to yellowish-brown, with an outer, hyaline unit wall and an inner laminated, yellowish-brown wall (Fig. 1J). However, the outer wall of the Australian collections may be ephemeral and an outer wall may be present in other collections in less-mature spores of

G. fuegianum. Further, the inner membranous wall develops as the sporocarp matures and is not always present. The figures of Yao *et al.* (1992) suggest a three-walled spore. Hall (1977) described a fungus with two walls, the outer thick, laminate and brown. The inner wall is thinner and hyaline to yellow. It would appear that the New Zealand collections may not be *G. fuegianum*. The diagrams of *G. fuegianum* in Thaxter (1922) resemble the fungus collected in Australia. While spore clusters are discrete in the Australian collections, they do not appear as raspberry-like structures of *G. fuegianum*. The morphology of sporocarps of the fungi from South America, New Zealand, UK and Australia is similar, but their relationship to each other needs clarifying.

Further, Australian collections vary. Those with relatively small spores tend to bruise readily and release a white exudate when hyphae are damaged, which presumably causes the adhesion of soil to the surface. The spores are paler than in specimens with relatively large spores and the inner membranous wall is common. However, both types of sporocarp have been collected within 1 m of each other and are assumed for the present to be the same species.

8. *Glomus fulvum* (Berkeley & Broome) Trappe & Gerdemann

Sporocarps rounded, up to 10 × 12 mm, mottled white to cream colour or pale brown, lacking a peridium, the spores on the surface easily detached.

Spores initially globose and developing terminally on hyphae 6–8 µm in diameter, later often becoming obovoid or clavate and 65–120 × 45–100 µm, with a single laminated, hyaline to pale brown wall 2–5 µm thick. Spore contents pale yellow, after spores attain full size and wall thickness, developing a septum attached squarely at the spore wall to separate spore contents from the subtending hypha. Subtending hyphae tapering slightly, 8–12 µm in diameter at the point of attachment, the wall single and thinning rapidly with distance from the spore, usually detached from glebal hyphae.

Glebal hyphae mostly empty in mature sporocarps, 6–22 µm in diameter, thin-walled.

Distribution, habitat and season

Apparently found worldwide, in Australia found from New South Wales, Queensland, Victoria and Western Australia in wet forests; February through to July, October.

Collections examined

NEW SOUTH WALES: Barrington Tops National Park, Mountaineer Trail, *J. Trappe & M. Castellano*, 29.iv.1992 (H5756). QUEENSLAND: Bluewater State Forest Site 3, *L. Cremler*, 13.iv.1989 (H4465). Cape York, 52 km from Weipa on road to Archer river, *J. Trappe* T15342, 11.iii.1995 (DAR). Closhey River Rd, *J. Trappe*, 6.ii.1992 (H5537). Gunawarra, Site 9, *N. Bougher*, 8.v.1991 (H4687). Kirrama Site 3, *N. Malajczuk*, 9.v.1991 (H4713). Kuranda, Site 4, *P. Reddell*,

6.v.1991 (H4620). Mount Baldy Site 2, *M. Castellano*, 7.v.1991 (H4629). Platypus Ck, *N. Malajczuk*, 2.vii.1988 (H4005). 12 km west of Mt Glorius, *R. Schaefer*, 4.v.1992 (H5963). VICTORIA: East Gippsland, Lind National Park, off Princes Hwy 3.8 km west of Lind Park Rd, *A. Claridge*, Trappe 19742, 14.x.1996 (MEL). WESTERN AUSTRALIA: Boranup National Park, beach end of Point Rd, *J. Trappe & M. Castellano*, Trappe 14802, 20.vii.1993 (DAR).

Remarks

These are the first reports of *Glomus fulvum* from Australia. It has been collected many times from scats of *Rattus* spp. Attempts to establish pot cultures from spores in scats have failed and the mycorrhizal status of the fungus remains unknown.

9. *Glomus macrocarpum* Tulasne & C.Tulasne

This species has been fully described elsewhere (Gerdemann and Trappe 1974) and is reported from South Australia (McGee 1986). We report an additional record of the sporocarpic form here.

Collections examined

NEW SOUTH WALES: Sydney, North Head, from a pot experiment inoculated with spores from scats of *Rattus* sp *G. Pattinson* NH 1.15, 13.xii.1997 (DAR).

10. *Glomus pubescens* (Saccardo & Ellis) Trappe & Gerdemann

Sporocarps rounded to lobed, up to 7 × 5 × 3 mm, the surface white and fluffy from a peridium of erect hyphae enclosing a firm, yellowish-brown gleba of randomly arranged blastospores.

Blastospores globose to obovoid or subclavate, 20–38 × 18–36 µm, with a single hyaline, laminate wall 1.5–4(–6) µm thick that does not swell in lactic acid but does in ammoniacal Congo red. Spore contents subhyaline to translucent pale yellowish-green, dense with large oil drops. Spore contents separated from the attached hypha by a swollen wall. Subtending hypha continuous with the spore wall, hyaline, 2–3 µm in diameter at the spore attachment and attached squarely with a slight flare, the lumen *c.* 0.5 µm broad.

Gleba of hyphae 1.5–2.5 µm in diameter with lumens 0.3–0.5 µm broad.

Distribution, habitat and season

New South Wales, under litter in rainforests, September.

Collections examined

NEW SOUTH WALES: Styx River State Forest near New England National Park, *P. A. McGee*, 25.ix.1989 (DAR 69438, 69439).

Remarks

This is the first report of *Glomus pubescens* from Australia. It is particularly interesting because of the apparent

confusion over the original identity of *D. tubaeforme* (see Warcup 1985). Chips of sporocarp were placed against the roots of a seedling of *Melaleuca uncinata*, a plant which forms both ecto- and arbuscular mycorrhizas, in sterile soil. The fungus germinated and fine hyphae grew around the root surface, but no mycorrhizas formed. Lack of mycorrhizas may have been due to edaphic factors; alternatively, this fungus may not produce mycorrhizas and is saprobic. Gerdemann and Trappe (1974) found it attached to sticks on the forest floor. The species differs from *D. tubaeforme* in spore shape and having a fluffy peridium and spores with coloured contents and thin walls.

The Australian collections have sporocarps up to $7 \times 5 \times 3$ mm, whereas those from North America do not exceed 1 mm in diameter (Gerdemann and Trappe 1974). No other significant morphological differences have been detected, however, and sporocarp size can vary strongly within a given species of *Glomus*. Accordingly, at least for the present, we regard the material from both continents as conspecific.

11. *Glomus tenerum* Tandy

This species has been fully described from several collections from South Australia (Tandy 1985; McGee 1986). It has not been recorded outside Australia. We report additional records here.

Collections examined

NEW SOUTH WALES: southern end of Royal National Park, *P. McGee*, 7.vii.1989 (DAR 74538, 75539). QUEENSLAND: Atherton, Mount Baldy Site 2, *M. Castellano*, 7.v.1991 (H4630). TASMANIA: west of Maydena, Westfield Rd, *M. J. Trappe*, 16.v.1991 (H5146). WESTERN AUSTRALIA: 25 km east of Denmark, *N. Malajczuk*, 4.ix.1984 (H0427).

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