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ABSTRACT

Gyroporus (Gyroporaceae, Boletales) is a highly diverse genus of poroid ectomycorrhizal mushrooms with a nearly worldwide distribution. Previous attempts to unravel the diversity within this genus proved difficult due to the presence of semicryptic species and ambiguous results from analysis of ribosomal RNA markers. In this study, we employ a combined morphotaxonomic and phylogenetic approach to delimit species and elucidate geographic and evolutionary patterns in Gyroporus. For phylogenetic analyses, the protein-coding genes atp6 (mitochondrial adenosine triphosphate [ATP] synthase subunit 6) and rpb2 (nuclear second largest subunit of RNA polymerase II) were selected based on their utility in studies of Boletales. We infer several distinct clades, most notably one corresponding to G. castaneus as a speciose Northern Hemisphere group, another unifying G. cyanescens and like entities, and a third group unifying G. longicystidiatus and a New World sister species. Also notable is the recovery of a sister relationship between the cyanescens and longicystidiatus clades. We formally describe five new species of Gyroporus, outline a number of provisional species, and briefly discuss distributional patterns. This study provides an important scaffold for future work on this well-known but poorly understood genus of fungi.

INTRODUCTION

Gyroporus Quélet (Gyroporaceae, Boletales) is a genus of ectomycorrhizal boletes with representatives on every major continent except Antarctica. These fungi are strongly implicated as symbionts with an array of ectotropic plants, including species of Pinaceae, Fagaceae, Myrtaceae, Fabaceae, and Phyllanthaceae, among others (Singer et al. 1983; Agerer 1999; Raidl et al. 2006; Ramanankierana et al. 2007; Yuwa-amornpitak 2009). Taxa within this group have been known since the 18th century (Bulliard 1787, 1788). Gyroporus sensu Quélet (1886) included some members that have since been excluded (Pateuillard 1900; Singer 1945). Its modern circumscription encompasses boletes with a yellow spore print, clamp connections, and circumferential to variously arranged (i.e., not longitudinal) stipe hyphae (Singer 1986; Watling 2008). The monophyly of this genus has been corroborated in previous studies (Binder and Bresinsky 2002; Wilson et al. 2011, 2012).

Despite the distinctiveness of this genus, its wide geographic distribution, and long formal history, much of the diversity of Gyroporus has yet to be elucidated. Previous phylogenetic studies on Gyroporus emphasized loci (i.e., ribosomal RNA markers) that yielded equivocal results at the infrageneric level (e.g., Wilson et al. 2011; Das et al. 2017). Imprecise taxonomy has also been a hindrance to progress on this genus, further confounded by the presence of many
semicryptic species. Collections from various parts of the world have generally been interpreted in relation to European species concepts (i.e., *G. cyanescens*, *G. castaneus*) or, to a lesser extent, North American ones (i.e., *G. subalbellus*). Here, we present a global phylogenetic overview of *Gyroporus*. Major results include the delimitation of multiple species and a sister relationship between the *cyanescens* and *longicystidiatus* clades. Five new species are described, three of which are known only from Australia and are closely related to *G. cyanescens*.

**MATERIALS AND METHODS**

*Morphology, vouchers, and names.*—Micromorphological, macromorphological, and ecological notes were made from fresh collections and herbarium material. Slides for microscopic study were prepared with water or 3% potassium hydroxide. Pileipellis and hymenium sections were studied. Stipitipellis morphology was observed but is not reported here, since it is highly variable and of limited diagnostic value in this genus. Q represents the mean length/width quotient of the spores. Specimens in this study are identified by field collection numbers and/or herbarium accession numbers (e.g., NY, TNS, MICH). Unless otherwise noted, the collections used here are housed at the following herbaria: NY, BR, TNS, TMI, MICH, and CFMR. Some collections may have duplicates housed at other institutions (e.g., CORT, FLAS, BRI, HMAS, MFLU, SDBR-CMU). Names that do not appear in MycoBank or are not formally described represent provisional names and are indicated as nom. prov.; these need additional study. Names given as *Gyroporus* sp. are based on two or fewer specimens.

The following geographic abbreviations are utilized in figures: USA (United States of America) with standard abbreviations for states (VT, FL, etc.), COL (Colombia), CR (Costa Rica), BLZ (Belize), CHN (China), JP (Japan), SKOR (South Korea), THAI (Thailand), PK (Pakistan), IT (Italy), BELG (Belgium), CMRN (Cameroon), SEN (Senegal), QLD (Queensland, Australia), and WAUS (Western Australia, Australia). Exemplars labeled with “gb” in figures were acquired from GenBank.

**DNA extraction, amplification, and DNA sequence alignment.*—Phylogenetic analyses included partial sequences of two protein-coding genes often used for systematic studies of the Boletales (Kretzer and Bruns 1999; Dentinger et al. 2010): the mitochondrial gene *atp6*, encoding the sixth subunit of adenosine triphosphate (ATP) synthase, and the nuclear gene *rpb2*, encoding the second largest subunit of RNA polymerase II. A list of *Gyroporus* specimens/sequences used in this study is provided (see SUPPLEMENTARY TABLE 1). DNAs were extracted from homogenized tissues of dried basidiocarps based on extraction protocols outlined in Hosaka and Uno (2011) and Kluting et al. (2014). DNA sequences were aligned, and new primers designed for *Gyroporus* using the default parameters in PRIMER 3 (Rozen and Skaletzky 1999). The partial mitochondrial *atp6* gene was polymerase chain reaction (PCR)-amplified with ATP6-1 (or ATP6-3) and ATP6-2 (Kretzer and Bruns 1999) or using primers designed for specific amplification of *Gyroporus* (ATP6gyro-F1: 5’-TTGAAGTTACAGTTTATTAAG-3’ and ATP6gyro-R1: 5’-CTGCTAAATTCACTASCTGTA-3’). The partial *rpb2* gene was initially PCR-amplified with degenerate primer sets fRPB2-5F/bRPB2-7R, fRPB2-5F/bRPB2-7R2 (Liu et al. 1999), and bRPB2-6f/bRPB2-7R2 (Matheny 2005). PCR amplification of *rpb2* also included primers designed specifically for the amplification of *Gyroporus* (rpb2gyro-F1: 5’-AAGAAGCTTACAGGGATGT-3’ and rpb2gyro-R1: 5’-YCCYTTRACASRNTGYTCC-3’). A total of 55 *atp6* and 38 *rpb2* sequences for *Gyroporus* were generated and have been deposited in GenBank under accession numbers MF818144–MF818236 (SUPPLEMENTARY TABLE 1).

PCR cycling conditions for *atp6* included an initial denaturation at 95 C for 5 min, followed by 40 cycles of 95 C for 30 s, 45 C for 90 s, and 72 C for 2 min, and a final extension at 72 C for 10 min. The cycling conditions for *rpb2* used an initial denaturation at 95 C for 5 min, followed by 35 cycles of 95 C for 30 s, 58 C for 1 min, and 72 C for 1 min, and a final extension at 72 C for 7 min.

**Phylogenetic analyses.*—Alignments of *atp6* and *rpb2* were performed using MUSCLE via the European Molecular Biology Laboratory European Bioinformatics Institute (EMBL-EBI) Web site (http://www.ebi.ac.uk/). Introns were removed from the *rpb2* alignment prior to phylogenetic analysis. The total lengths of the alignments for phylogenetic analyses were 710 and 922 bp for *atp6* and *rpb2*, respectively. Bayesian analysis for each gene was performed with MrBayes 3.2.6 (Ronquist et al. 2012) on the CIPRES Science Gateway 3.1 (Miller et al. 2010) using a generalized time-reversible model with gamma-distributed rate variation between sites. The priors utilized were defaults in MrBayes. Metropolis-coupled Markov chain Monte Carlo analyses were run with default settings (runs = 2, nchains = 4, swapfreq = 1, nswaps = 1) for 20 million generations, which was
sufficient for convergence (convergence diagnostic: 0.0015–0.0023). The proportion of samples discarded as burn-in was 25%. A secondary Bayesian analysis was conducted for atp6 with a reduced number of terminals (analysis identical except the alignment was reduced from 59 to 36 terminals). Maximum likelihood (ML) analyses were conducted, following procedures outlined in Kluting et al. (2014), although atp6 and rpb2 were analyzed separately, not combined. ML analyses were conducted using 1000 bootstrap replications. Alignments are deposited in TreeBASE (study 21499).

RESULTS

Bayesian analysis of atp6 sequences (FIG. 1) inferred two major clades of Gyroporus: one unifying G. cyanescens, G. longicyistidiatus, and like entities (including the lineage represented by OR182 and BOS472), the other unifying G. castaneus, G. mcnabbi, sp. nov., and the clade consisting of G. naranjus, nom. prov., and African exemplars (TH9913, Thoen7634). The secondary Bayesian atp6 analysis recovered the same major relationships and increased the posterior probabilities at several nodes, two of which are included and indicated with asterisks (FIG. 1). Bayesian analysis of rpb2 sequences (FIG. 2) inferred nested clades of Gyroporus and also recovered the clade unifying G. cyanescens, G. longicyistidiatus, and like entities (including the lineage represented by OR182 and REH8805). The clade unifying G. cyanescens, G. longicyistidiatus, and like entities is denoted as clade b in the phylograms (FIGS. 1, 2). In the rpb2 analysis, the G. castaneus, G. mcnabbi, sp. nov. (+ G. subalbellus + OR801, OR870), and G. naranjus, nom. prov. (+ TH9913, Thoen7634), clades were each maintained as distinct similar to the atp6 analysis, but unlike the atp6 analysis they did not together form a larger clade distinct from clade b. The G. castaneus clade is denoted as clade a in the phylograms (FIGS. 1, 2). ML analyses were comparable to the Bayesian analyses, recovering the same species and key clades, although in the ML rpb2 analysis G. mcnabbi, sp. nov., G. subalbellus, and OR801/OR870 were not recovered together in a single clade as in the Bayesian rpb2 analysis.

TAXONOMY

Gyroporus australiensis Davoodian, Fechner & Halling, sp. nov. FIGS. 3–5
MycoBank MB822346

Typefication: AUSTRALIA. QUEENSLAND: Great Sandy National Park, Fraser Island, near Lake McKenzie, 25°27′50″S, 153°04′14″E, 97 m, 18 May 2011, R.E. Halling 9501 (holotype BRI, isotype NY).

Diagnosis: Differs from other species of Gyroporus in Australia by the brown to light brown pileus and gradual cyanescent reaction that is present in the flesh and on the pores but absent from the tubes.

Etymology: australiensis (Latin), in reference to the place (Australia) of origin.

Pileus 3.5–8.5 cm broad, convex to plane, margin even to slightly projecting, sometimes slightly incurved when young, dry, matted fibrillose to tomentose to squamulose/subscaly, brown to cinnamon to light brown to light peach brown (brown in dried condition), often over whitish to yellowish background. Flesh white, slowly bluing (pale blue very gradually to darker blue), although rarely rapidly and intensely cyanescent (REH 9492), with mild odor and taste. Tubes adnexed, white to off-white to yellowish at first, light and clear yellow to yellowish white to creamish with age, generally not cyanescent, although sometimes bluing slightly in areas, with pores concolorous and cyanescent (rarely intensely so: REH 9492). Stipe 2–7 cm long, 0.7–2 cm broad, straight or curved, subequal to subclavate, sometimes ventricose, sometimes pinched or tapered at base, dry, finely submentosely to matted tomentose, sometimes appearing with annular zone, subconcolorous to concolorous with pileus over white to off-white to yellowish background, slowly bluing when injured, pithy at first, becoming cavernous-hollow.

Spores (6.5–)7.2–9.9(–11.9) × (4.5–)5.4–6.3 μm (Q = 1.8), smooth, yellow-hyaline, ellipsoid to subovoid to subreniform to reniform (the larger spores some- times appearing with annular zone, subconcolorous to concolorous with pileus over white to off-white to yellowish background, slowly bluing when injured, pithy at first, becoming cavernous-hollow.

Ecology and distribution: Gregarious to scattered to solitary. On sand in sclerophyll habitat with species of Myrtaceae and Casuarinaceae. Known only from Fraser Island and nearby Cooloola. Mar to Jun.

Other specimens examined: AUSTRALIA. QUEENSLAND: Great Sandy National Park, Cooloola, Freshwater Road, 25°57′04.0″S, 153°08′06.0″E, 150 m, 25 May 2011, R.E. Halling 9559 (NY, BRI); Fraser Island, 4.8 km along Woralie Road, 25°13′07.0″S, 153°13′22.8″E, 171 m, 18 May 2010, R.E. Halling 9312 (NY, BRI); Road from Eurong to Central Station, 25°30′01.1″S, 153°06′07.2″E, 82 m, 17 May 2011, R.E. Halling 9492 (NY, BRI); Cornwell’s Road, 25°24′40.3″S, 153°02′42.0″E, 68 m, 10 Jun 2009, R.E. Halling 9226 (NY, BRI); 1–2 km SE of Kingfisher Bay, 25°23′38.8″S, 153°01′48.0″E, 30–35 m, 9
Figure 1. Consensus phylogram from Bayesian analysis of atp6 sequences. Bayesian posterior probabilities are at the nodes (values with asterisks are from the secondary analysis). Bootstrap values from ML analysis of atp6 sequences are included after the posterior probabilities. Included in the analysis but cropped from this image are outgroup sequences for Hygrophoropsis aurantiaca (GLM45936) and Suillus spraguei (MB03-93) acquired from GenBank and Suillus umbonatus (REH8715). Scale bar shows substitutions/site. Letters at nodes indicate the following clades: a = G. castaneus clade; b = clade unifying the cyanescens clade, longicystidiatus clade, and a clade of undescribed species including OR182; c = cyanescens clade + longicystidiatus clade; d = cyanescens clade, containing G. cyanescens and related clades, including a clade of new species from Australia; e = longicystidiatus clade, containing G. longicystidiatus and G. paralongicystidiatus, sp. nov.
Mar 2011, R.E. Halling 9482 (NY, BRI); Road from Eurong to Central Station, 25°30’14.0"S, 153°06’57.6"E, 30 m, 6 Mar 2011, R.E. Halling 9460b (NY, BRI); Cornwell’s Road, 25°24’06.8"S 153°01’51.6"E, 48 m, 24 May 2010, R.E. Halling 9361 (NY, BRI); track from Central Station to Lake Birrabeen, 25°29’42.7"S, 153°03’54.0"E, 138 m, 4 Jun 2009, R.E. Halling 9151 (NY, BRI).

Comments: Gyroporus australiensis is the only cyanescens G. cyanescens known so far from Australia with a distinctly brown pileus, which is especially apparent in dried condition. Many other G. cyanescens–like entities in Australia exhibit a straw yellow pileus suggestive of “classical” G. cyanescens of Europe and the Northern Hemisphere (e.g., G. austrocyanescens, nom. prov. [FIGS. 1, 2], G.

Figure 2. Consensus phylogram from Bayesian analysis of rpb2 sequences. Bayesian posterior probabilities are at the nodes. Bootstrap values from ML analysis of rpb2 sequences are included after the posterior probabilities. Included in the analysis but cropped from this image are outgroup sequences for Hygrophoropsis aurantiaca (MB03-127) and Suillus spraguei (MB03-002) from GenBank. Scale bar shows substitutions/site. Letters at nodes indicate the following clades: a = G. castaneus clade; b = clade unifying the cyanescens clade, longicystidiatus clade, and a clade of undescribed species including OR182; c = cyanescens clade + longicystidiatus clade; d = cyanescens clade, containing G. cyanescens and relatives; e = longicystidiatus clade, containing G. longicystidiatus and G. paralongicystidiatus, sp. nov.
Gyroporus brunnescens Davoodian, Fechner & Halling, sp. nov. 

**Typification**: AUSTRALIA. QUEENSLAND: Great Sandy National Park, Fraser Island, road from Eurong to Central Station, 25°30′01″S, 153°06′07″E, 82 m, 17 May 2011, R.E. Halling 9491 (holotype BRI, isotype NY).

**Diagnosis**: Differs from other species of *Gyroporus* by exhibiting a distinct brown oxidation reaction in exposed tissues.

**Etymology**: *brunnescens* (Latin), in reference to the brown oxidation reaction where tissues are exposed.

Pileus 2–6 cm broad, convex to plano-convex to uplifted, dry, heavily appressed fibrillose to tomentose to felty, sometimes subsquamulose, yellowish brown to grayish yellow to light yellow, staining light brown or unstaining. Flesh white to pale yellow, staining pale pinkish brown to dark brown, with mild odor and taste. Tubes adnexed to adnate, white to whitish to very pale greenish yellow to yellow, staining pale pinkish brown to dark brown (especially on pores). Stipe 1.5–6 cm long, 0.9–2.5 cm broad, equal, tapered at base, nearly concolorous with pileus, although white background often more apparent on stipe, dry, appressed fibrillose to finely matted subfelty with matted squamules at base, sometimes appearing with annular zone, staining brown, pithy becoming chambered.

Spores (6.4–)8–11.2(–12) × (4–)4.4–4.8(–5.6) µm (Q = 2.05), smooth, yellow-hyaline to nearly so, elliptical to subelliptical to subreniform to subovoid, generally elongate, sometimes appearing apiculate. Basidia 28–33 ×

Ecology and distribution: Gregarious to scattered to solitary in association with species of Myrtaceae and Casuarinaceae. Known from localities in Great Sandy National Park and Davies Creek National Park, Queensland. Feb to May.

Other specimens examined: AUSTRALIA. QUEENSLAND: Davies Creek National Park, Davies Creek Road, 17°01′36.1″S, 145°36′03.6″E, 713 m, 11 Mar 2007, R.E. Halling 8908 (NY, BRI); Great Sandy National Park, Cooloola, Freshwater Road, 25°56′37.0″S, 153°07′22.8″E, 154 m, 23 May 2011, R.E. Halling 9545 (NY, BRI); Fraser Island, road from Pile Valley to Lake McKenzie, 25°28′12.0″S, 153°04′12.0″E, 90 m, 9 Mar 2011, R.E. Halling 9479 (NY, BRI); Wanggoolba Road west of Central Station, 25°28′41.5″S, 153°02′49.2″E, 54 m, 15 Feb 2011, R.E. Halling 9414 (NY, BRI).

Comments: This is the only Gyroporus known to have a distinct brown oxidation reaction with no cya-
nescentine stage. It is phylogenetically embedded in the clade unifying G. cyanescens and relatives.

Gyroporus furvescens Davoodian & Halling, sp. nov.  
MycoBank MB822348

Typification: AUSTRALIA. QUEENSLAND: D’Aguilar National Park, vicinity of Mt. Glorious, Maiala area walking tracks, 27°20′00″S, 152°45′48″E, 680 m, 8 Mar 2012, R. E. Halling 9673 (holotype BRI, isotype NY).

Diagnosis: Differs from other cyanescent species of Gyroporus in Australia by the oxidation reaction that is deep blue then nearly black and unique appearance in dried condition (surfaces blackish to deep blue to sometimes purplish).

Etymology: furvescens (Latin), becoming dark, in reference to the deep blue to nearly black oxidative reaction.

Pileus 2–12 cm broad, convex to plano-convex, dry, appressed squamulose-scaly to flattened lanose to matted fibrillose, yellow-white to yellow-brown to cinnamon brown, quickly cyanescent (eventually to nearly black or very dark brown). Flesh white, quickly and intensely deep blue sometimes with lilac and/or violet, with mild odor and taste. Tubes adnexed, whitish at first, becoming pale yellow, with pores likewise and only the pores cyanescent, although tubes occasionally patchily cyanescent. Stipe 3–9 cm long, 0.8–3 cm broad, subclavate to clavate, dry, often with annular zone (sometimes very faint to nearly absent), finely matted pubescent above, appressed fibrillose to appressed sublanose below, yellowish white above, brownish below, quickly cyanescent (eventually to nearly black), chambered.

Spores (5.6–)6.8–8.1(−9) × (3.2–)3.4–4.7(−4.8) µm (Q = 1.71), smooth, yellow-hyaline, subreniform to reniform to ellipsoid to subovoid, sometimes appearing apiculate. Basidia 30–33 × 9.5–12 µm, clavate. Cheilocystidia 22–24(32) × (5)5.5–6.5(9.5) µm, fusoid. Undifferentiated hymenial elements 16–24 × 3–8 µm, clavate to cylindrical. Pileipellis of elongated, repent elements; elements compactly to loosely bundled; terminal cells with more or less rounded or tapering ends. Clamp connections present.

Ecology and distribution: Solitary or cespitose on soil with species of Eucalyptus and Lophostemon. Thus far known only from three collections in southeastern Queensland. Feb to Mar.

Other specimens examined: AUSTRALIA. QUEENSLAND: D’Aguilar National Park, vicinity...
of Mt. Glorious, 27°17′45.2″S, 152°43′40.8″E, 601 m, 20 Feb 2013, R.E. Halling 9807 (NY, BRI); Main Range National Park, Cunningham’s Gap, 28°02′58.9″S, 152°23′38.4″E, 760–770 m, 3 Mar 2012, R. E. Halling 9662 (NY, BRI).

Comments: Gyroporus furvescens is especially distinguishable by the appearance in dried condition, where the pileus and stipe surfaces are stained black, deep blue, slate blue, or sometimes purplish over gray to very pale yellow ground. This appearance seems to persist for at least several years in herbarium specimens.

Gyroporus mcnabbii Davoodian, Bougher & Halling, sp. nov.  
Mycobank MB822349

Typification: AUSTRALIA. QUEENSLAND: D’Aguilar National Park, vicinity of Mt. Glorious, 27°17′45.2″S, 152°43′40.8″E, 601 m, 20 Feb 2013, R.E. Halling 9808 (holotype BRI, isotype NY).

Diagnosis: Differs from other species of Gyroporus in Australasia by the darkly colored subvelutinous pileus and stipe surfaces, which sometimes appear mottled.

Etymology: mcnabbii (Latin), named in honor of New Zealand mycologist, R. F. R. McNabb.

Pileus 2–9 cm broad, convex to plano-convex, dry, dark chestnut brown to cinnamon brown to brownish orange to brownish red, with these colors sometimes forming a mottled appearance, subvelutinous to finely submentose to roughly furfuraceous. Flesh white, unchanging, with mild odor and taste. Tubes adnexed, 4–8 mm long, white to creamish becoming pale yellow, sometimes discoloring to orange. Stipe 2.5–6 cm long, 0.5–2.9 cm broad, equal to subclavate, sometimes pinched at the base, dry, subvelutinous to finely submentose to subpruinose, subconcolorous to concolorous with pileus, white to faint orange to faint pinkish at base, with interior white, unchanging, pithy to chambered to hollow, with annular zone especially apparent when a button (faint to absent in maturity). Spore print yellow to bright yellow.

Spores (7.6–)8.4–10.7(–11.9) × (4.9–)5.5–6.7(–7) µm (Q = 1.61), smooth, yellow-hyaline, ellipsoid to subovoid, sometimes subreniform, sometimes appearing minutely apiculate. Basidia 24–30 × 9.5–11.5 µm, clavate. Cheilocystidia 25–40 × 6–9 µm, versiform (fusoid, elongated ventricose-rostrate, narrow subcylindricl). Pileipellis a dense trichoderm. Clamp connections present.

Ecology and distribution: Solitary to cespitose to gregarious to scattered with species of Myrtaceae (Eucalyptus, Leptospermum) and possibly Casuarinaceae and Fabaceae (Acacia). Known from Australia and New Zealand. Jan to Jun.

Other specimens examined: AUSTRALIA. QUEENSLAND: Great Sandy National Park, Cooloola, Freshwater Road, 25°57′13.3″S, 153°06′0.0″E, 152 m, 11 Mar 2012, R.E. Halling 9677 (NY, BRI); Davies Creek National Park, Davies Creek Road, ±8.5 km from Kennedy Highway, 17°01′36.1″S, 145°35′24.0″E (coordinates are of area formerly known as Rope Swing Lunch Site), 670 m, 22 Mar 2007, R.E. Halling 8955 (NY, BRI); Route 97, near Queensland–New South Wales border, 28°15′27.0″S, 153°14′09.6″E, 160 m, 5 Jun 2007, R.E. Halling 8979 (NY, BRI); NEW SOUTH WALES: Gibraltar Range National Park, along Gwydir Highway, 2 May 1992, leg. M.A. Castellano E 4600 (PERTH); Central Coast, Palm Grove, 7 km W of intersection of Pacific Highway and Ourimbah Creek Road, O’Sullivan’s Way, 33°19′54.8″S, 151°18′28.8″E, 64 m, 10 Mar 2017, R.E. Halling 10126 (NY, DAR); WESTERN AUSTRALIA: Perth, Victoria Road, ±31°52′53.8″S, ±116°07′37.4″E, 14 Apr 2005, leg. K. Griffths E8155 (PERTH); TASMANIA: Forest Resources Mycorrhiza Site, 20 Mar 1993, leg. N. Malajczuk E843 (PERTH); NEW ZEALAND. AUCKLAND: Titirangi, Clark Bush, 13 Jun 1973, leg. S. Haydon 30836 (PDD); Atkinson Park, 11 Jan 1966, leg. R.F.R. McNabb 25065 (PDD).

Comments: Gyroporus mcnabbii is a distinctive species that appears to have a wide range through Australia and New Zealand. The deep, sometimes mottled colors and subvelvety texture distinguish it from other superficially castaneus-like entities in the region. Other New Zealand specimens referenced for this description but not studied in detail were PDD 25066 (leg. R.F.R. McNabb) and PDD 29553 (leg. P.J. Brook). McNabb (1968) treated his New Zealand collections as G. castaneus, and his description of the material agrees strongly with the material examined here.

Figure 9. Gyroporus mcnabbii (holotype R.E. Halling 9808). Photo: Roy Halling.
Gyroporus paralongicystidiatus Davoodian, sp. nov.

MycoBank MB822350

Typification: COSTA RICA. SAN JOSÉ: Dota, ±5 km SW of Cerro de la Muerte, Albergue de Montaña, Savegre, 2200 m, 9 Jul 2001, R.E. Halling 8274 (holotype US), isotype NY).

Diagnosis: Differ from other species of Gyroporus in the Americas by the combination of the tomentose to finely matted pileus, brown to light brown to pinkish brown coloration, and conspicuous cheilocystidia in early maturity.

Etymology: paralongicystidiatus (Greek), near longicystidiatus.

Pileus 4–5 cm broad, plane to slightly convex, sometimes slightly concave with maturity, dry, brown to light brown to pinkish brown, woolly tomentose to fine matted, sometimes forming very fine squamules or furfur. Flesh white, unchanging. Tubes adnexed, whitish to cream to yellow, with concolorous pores. Stipe 3–6.5 cm long, 1–1.5 cm broad, more or less equal, slightly tapered at base, more or less concolorous with pileus or paler, subtomentose to roughly glabrous, pithy to chambered to hollowing.

Spores (7–)8.2–9.8(–10.5) × (4.4–)5.1–5.7(–6.4) µm (Q = 1.63), smooth, yellow to yellow-hyaline, ellipsoid to subovoid to subreniform, occasionally shaped more or less like an unshelled peanut, sometimes appearing apiculate. Basidia 27–33 × 9–12 µm, clavate. Cheilocystidia 17–55 × 6–13 µm, versiform (fusoid, tapered toward apex, ventricose-rostrate, obclavate, cylindrical, subutriform, sublageniform, roughly cylindrical with slightly inflated apex), especially noticeable in early maturity, somewhat obscured with advanced maturity as other hymenial elements develop. Pileipellis an elongated, dense, tangled, sublageniform, roughly cylindrical with slightly inflated apex, especially noticeable in early maturity, somewhat obscured with advanced maturity as other hymenial elements develop. Pileipellis an elongated, dense, tangled, collapsing trichodermium. Clamp connections present.

Ecology and distribution: Solitary to scattered on soil. Known from Costa Rica under Quercus seemannii and Quercus copeyensis and Colombia in mixed forest with Quercus humboldtii. May, Jul, and Nov.

Other specimens examined: COSTA RICA. SAN JOSÉ: Dota, ±5 km SW of Cerro de la Muerte, Albergue de Montaña, Savegre, 2200 m, 10 Jul 2000, Halling 8002 (NY); same locality as previous, 18 Jun 1997, Halling 7725 (NY); same locality as previous, 24 Nov 1993, Halling 7190 (NY). COLOMBIA. CAUCA: Tunia, Corregimiento El Mango, Reserva Natural "El Guayabo," 1640 m, 28 May 1991, A.E. Franco-Molano 498 (NY).

Comments: Gyroporus paralongicystidiatus, known only from three collections in the northern neotropics, is phylogenetically sister to G. longicystidiatus Nagasawa & Hongo from East Asia (Nagasawa 2001) and geographically separated. Several exemplars of the latter were examined, including a paratype (EN99-67). The Colombian specimen roughly agrees with the type morphology, and its atp6 sequence is identical to the type, although the surfaces of the Colombian specimen are lighter in color and the pileipellis is shorter. Additional collections are needed to ascertain the geographic extent and morphological variation of this species.

DISCUSSION

The sister relationship between the cyanescens and longicystidiatus clades is a key result (node c in FIGS. 1, 2). Given the subdued brownish colors of G. longicystidiatus, along with the lack of oxidation reactions, previous researchers have assumed this and similar species to be closer to G. castaneus. The evidence presented here, however, places G. longicystidiatus phylogenetically closer to G. cyanescens. This is likely one of the reasons for confusion in previous systematic studies of Gyroporus, since many collections of G. longicystidiatus and similar entities (e.g., G. paralongicystidiatus, Gyroporus sp. BOS472) were originally determined as G. castaneus.

Species in the cyanescens, longicystidiatus, and “OR182” clades (together constituting clade b in FIGS. 1, 2) are morphologically comparable in their pileipellis structure, which is always a dense elongated trichodermium, i.e., the pileus is a mat of fibrils. This is most apparent in the cyanescens clade (node d in FIGS. 1, 2), where species are often very strongly tomentose, the fibrillosity being greatly elongated and somewhat clumped. In G. longicystidiatus and like entities (i.e., G. paralongicystidiatus and the clade including OR182, which is somewhat comparable to G. longicystidiatus in appearance), the dense fibrillosity is generally shorter than in the cyanescens clade and can be clearly visualized with a dissecting microscope; G. longicystidiatus was originally described as “tomentose to floccosely squamulose” (Nagasawa 2001). The trichodermium is often intensely tangled in the longicystidiatus clade (node e in FIGS. 1, 2). The remaining Gyroporoi (G. castaneus, G. naranjus, nom. prov., etc.) display a variety of trichoderms: more or less palisadal, erect/tangled, short, or elongated as discussed above, with rounded, tapered, or cystidioid end cells.

The Australian cyanescens group (i.e., the Australian clade within clade d in FIGS. 1, 2) is composed of two major clades, one of light-oxidizing and one of dark-oxidizing species. The light-oxidizing species are represented by the clade including G. australiensis, G. allocyanescens, nom. prov., and G. robinsonii, nom. prov. In these species the bluing reaction on injured flesh is gradual, initially turning slowly light blue then slightly intensifying over time. The dark-oxidizing species are represented by the clade including G. furvescens, G. austrocyanescens, nom. prov., G. neocyancens, nom.
Gyroporus castaneus 2017 remains formally 'G. castaneus 2015 (2010)' samples from Florida as well as group is sister to its Northern Hemisphere relatives 21995 1993 Gyroporus castaneus 1ng work at the herbarium. The Gyroporus species, which are mycorrhizal with G. occidentalis sensu lato several 2 http://orcid.org/0000-0002-4469-8303 http://orcid.org/0000-0002-8426-2133 Italian and Belgian exemplars (here. The Australian species display various biogeographic affinities: G. naranjus, nom. prov., is sister to African Gyropori (FIGS. 1, 2) and the Australian cyanescens group is sister to its Northern Hemisphere relatives (FIGS. 1, 2). Further sampling of G. cyanescens in the Northern Hemisphere is needed to confidently determine where G. cyanescens sensu stricto should apply. The G. castaneus clade (node a in FIGS. 1, 2) is a species complex that is widespread in the Northern Hemisphere. It includes representatives from Europe and North America (including Central America) as well as eastern Eurasia. Gyroporus purpurinus, an iconic purplish red North American species, is also a member of this clade (FIG. 2). The G. castaneus clade is highly diverse in North America, with at least three distinct undescribed lineages represented here. Gyroporus castaneus sensu stricto would appropriately be applied to the European lineage represented by the Italian and Belgian exemplars (FIGS. 1, 2), although it should be noted that the presence of other G. castaneus lineages in Europe is possible. The species has been neither neo- nor epitypified. Gyroporus castaneus sensu lato can be applied to clade a in its entirety (FIGS. 1, 2). Our study has excluded from Gyroporus castaneus sensu lato several lineages previously assumed to be G. castaneus or an infraspecific taxon, among them G. mcnambii, G. naranjus, nom. prov., the African exemplars TH9913 and Thoen7634, and the lineages represented by OR182 and BOS472. Further studies with additional sampling are needed to fully reveal the diversity of the G. castaneus clade in North America and worldwide.

Much of the diversity of Gyroporus remains formally undescribed. Some provisional taxa appearing here will remain undescribed until additional exemplars are collected; others will be described in forthcoming publications.

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