**Geodina (Pezizomycetes: Wynneaceae) has a single widespread species in tropical America**

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- Pezizales
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- synonym
- taxonomy

**Abstract:** Geodina salmonicolor is shown to be a synonym of *G. guanacastensis*, the type and only species of the genus. Comparisons of ITS rDNA sequences of a paratype and two recent collections of *G. guanacastensis* with published ITS sequences of *G. salmonicolor*, from the Dominican Republic, show that these are nearly identical. When *G. salmonicolor* was erected no sequences of the type species were available. Morphological comparisons supports the conspecificity. Details regarding the description of *G. salmonicolor* are pointed out. A four-gene phylogeny places Geodina and Wynnea as a supported sister group to the rest of the Sarcoscyphaceae. Species in these genera share morphological traits of cyanophobic spore markings, dark angular outer excipular cells that give rise to hairs and the origin of several apothecia from a common basal stalk. Their occurrence on soil rather than on wood or plant material distinguish them from other Sarcoscyphaceae. Based on morphology, phylogenetic relationships and trophic interactions we erect a new family, Wynneaceae, for *Geodina* and *Wynnea*.

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**INTRODUCTION**

The genus *Geodina* (Denison 1965), described more than 50 years ago, has remained an enigmatic taxon. The original and only species, *G. guanacastensis*, seemingly was not recollected until recently. It was placed in the Sarcoscyphaceae because of ascus form, anatomical details of the ascoma and hymenial coloration but, unlike other members of the Sarcoscyphaceae, it is distinctive because of its occurrence on soil. Other Sarcoscyphaceae are found on wood and plant material. In recent years a few collections of *G. guanacastensis* have come to light. Originally described from collections from Costa Rica there have been records and postings of *G. guanacastensis* from Florida, USA, and Mexico (Ortega-Lopez et al. 2019, Mushroom Observer: Observations 187260, 296893, 357225). These recent findings provide some insight into the distribution and the taxonomy of this species. This investigation was undertaken to determine the identity of several recent collections and to evaluate the recently described species, *G. salmonicolor* (Angelini et al. 2018), from the Dominican Republic.

*Geodina salmonicolor* was said to be distinguished from *G. guanacastensis* by hymenial color, pink salmon to pale pink-orange vs. pale orange to light yellow-orange, and larger ascospores (35–39 × 11–13 μm vs. 22–25 × 11–13 μm) (Angelini et al. 2018). Angelini et al. (2018) did not report examining the holotype or other material of *G. guanacastensis*. Using ITS and 28S rDNA sequences from the Dominican collections they were able to place their species in a clade with *Wynnea* in the Sarcoscyphaceae. In this paper we report on a recently collected specimen of *G. guanacastensis* and an ITS sequence obtained from a paratype of *G. guanacastensis*. In light of sequence data and a detailed morphological study we reconsider the identity of *G. salmonicolor*. We provide a revised description and illustrations of *G. guanacastensis*. We have studied and compared species of *Wynnea* and *G. guanacastensis*. Our goals in this study were to determine the species identity of these collections; to further investigate the relationship between *Wynnea* and *Geodina*; and to highlight the shared phylogenetic and morphological characteristics of the species in these two genera.

**MATERIALS AND METHODS**

**Material studied**

- **Bahamas:** Hardwood forest near Albany, New Province, Nassau, 2 Dec. 2017, *D. Maillis*. Specimen deposited at Leon Levi Native Plant Preserve, Banks Road, Eleuthera, Bahamas.
- **Costa Rica:** Kilometre 135, Pan American Highway no[rth] of Punta Arenas, Guanacaste Province, Denison *et al.* 2278, 13 Sep. 1964 (CUP-CA 81, holotype); Playa del Coco, Guanacaste, alt 200 ft, *Denison et al.* 2310, 14 Sep. 1964 (CUP-CA 84); Caña, Guanacaste Province, alt 150 ft., *Denison et al.* 2294, 13 Sep. 1964 (CUP-CA 83, CUP-CA 82). [A note on these collections. Even though we were unable to study these collections because of their ravaged condition we cite them to aid future researchers. A small fragment of CUP-CA 84 was used in the molecular work]. A collection of *Geodina* from Everglades National Park, Florida, USA was reported on the Mushroom Observer website (https://mushroomobserver.org/observer/show_observation/357225). The ITS DNA sequence data from this specimen, determined by Arian Farid, University of Southern Florida, was included in our study.
Molecular techniques

The new DNA sequences that contributed to this phylogenetic study were obtained from either DNA extraction of ascomata or previously extracted genomic DNA stocks that had been kept at -20 °C (Table 1). DNA extraction from ascomata utilized the Qiagen DNeasy Plant Mini kit (Germantown, MD cat #69104) as previously described (Pfister & LoBuglio 2018). PCR amplification utilized the following primer combinations: primer pair ITS1F, ITS2, ITS3 and ITS4 (Gardes & Bruns 1993, White et al. 1990) for the internal transcribed spacer region plus 5.8S gene (ITS); primer pair LROR and LR7 (Moncalvo et al. 2000) for the large subunit ribosomal RNA gene (28S); primers NS1, NS4, SL344, SL122 and NS8 (Landvik et al. 1997, White et al. 1990) for the small subunit ribosomal RNA gene (18S); primers RPB2-P6Fa and RPB2-P7Ra (Hansen et al. 2005) for the DNA-directed RNA polymerase II second largest subunit gene (RPB2); and either primer pairs EF1-983F and EF1-2218R or EF1-983F and EF1-1567R (Rehner 2001, Rehner & Buckley 2005) for the translation elongation factor 1-α gene (EF).

The RPB2 and EF gene regions were difficult to amplify from the herbarium samples of Wynnea species included in this study. Since a phylogenetic relationship between Wynnea and Geodina was initially established from phylogenetic analysis of the 28S rDNA, it allowed specific primers to be designed and successfully implemented in PCR. For the RPB2 region specific primers were designed based on the Geodina RPB2 DNA sequence. The sequence for the RPB2 specific primers are: GG3_RPB2-6F 5’-GCCTGACATAAGTTGGGAACA-3’, GG3_RPB2-7R 5’-CCATGGCCGATTGATATGTGT-3. The EF gene was successfully amplified for Wynnea macrotis. This sequence was used to design Wynnea specific primers for the EF gene. The sequences for the EF specific primers are: WM2_EF-983F 5’-TACTGGTATCCAGGCT-3’, and WM2_EF-1567R 5’-GCCTGACATAAGTTGGGAACA-3’. The NCBI primer designing tool (https://www.ncbi.nlm.nih.gov/tools/primer-blast/) was used to design these specific primers.

PCR amplifications were carried out in a BIO-RAD thermocycler. For PCR, 5 µL of 1/10 and 1/100 dilutions of the DNA extracts were used as templates in a total reaction volume of 25 µL. BIO-RAD iProof High-Fidelity PCR Master Mix (Hercules, CA, cat #1725310) was used for PCR amplification of the ITS, 28S, 18S, and EF gene regions. For the ribosomal DNA regions the PCR cycling parameters followed the BIO-RAD recommendations for iProof High-Fidelity DNA Polymerase and were as follows: 94 °C for 3 min, then 35 cycles of 94 °C for 5 seconds, a primer annealing step at 53 °C for 30 s, an extension at 72 °C for 30 s, followed by a final elongation step at 72 °C for 5 min and a 4 °C soak. The PCR reactions of the RPB2 region were most successful using Invitrogen Platinum Taq DNA Polymerase High Fidelity (Invitrogen, Thermo Fisher Scientific, Waltham, MA, cat # 11304011). For RPB2, the PCR cycling parameters were as follows: 94 °C for 3 min, then 35 cycles of 94 °C for 45 s, a primer annealing step at 52 °C for 45 s, an extension at 72 °C for 1:30 min, followed by a final elongation step at 72 °C for 10 min and a 4 °C soak.

Multiple bands were often present from RPB2 and EF PCR products. In these cases, the bands of interest were excised from 2 % agarose gels and purified using the Qiagen Gel extract kit (Germantown, MD cat # 28704). PCR product of all genes were sent to GeneWiz Inc. sequencing facilities (Cambridge, MA) for Sanger Sequencing. The forward and reverse sequences from each PCR product were edited using Sequencher v. 5.1 (GeneCodes, AnnArbor, Michigan). Sequences are deposited in GenBank and listed in Table 1.

The QIAamp DNA micro kit (Qiagen cat. #56304) was used to extract material from a paratype of G. guanacastensis (CUP-CA 84) because tissue sampling was very limited (approximately 1 mm square). PCR amplification of the ITS utilized the same procedures as above using the primer pairs ITS1F–ITS2 and ITS3–ITS4 and the BIO-RAD iProof High-Fidelity PCR Master Mix. The ITS DNA sequence of this type specimen was compared to our recent Geodina collection and to the sequence of G. salmonicolor reported by Angelini et al. (2018) using the alignment feature in NCBI BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi).

DNA sequence and phylogenetic analyses

A phylogenetic analysis of the four-gene (EF, 28S, RPB2, and 18S) concatenated data was assembled. DNA sequences were aligned using MUSCLE v. 3.7 and the model of nucleotide substitution was determined using jModelTest2 on XSEDE through the CIPRES Science Gateway (Miller et al. 2010). The four-gene data matrix included 23 taxa from the families Sarcoscyphaceae, Sarcomatosaceae, Chorioactidaceae and the outgroup taxa Marchella elata and Gyromitra californica (Table 1). Phylogenetic analyses were performed using Maximum likelihood (ML) and Bayesian analyses through the CIPRES Science Gateway (Miller et al. 2010). Both phylogenetic methods used the GTR+I+G model of sequence evolution. The ML analyses used RAxML-HPC2 on XSEDE (v. 8.2.12) (Stamatakis 2014) using the default parameters, and branch support was determined by 1 000 bootstrap replicates. Bayesian inference used MrBayes v. 3.2.6 (Huelsenbeck and Ronquist 2001) and consisted of four Markov chain Monte Carlo (MCMC) chains initiated from random trees for 10 000 000 generations and with tree sampling every 200 generations. The first 25 % of trees were discarded as the burn-in phase of each analyses, and posterior probability (PP) values were determined from the remaining trees. Single gene ML trees were determined for each of the 4 gene regions for comparison with the four-gene phylogeny to determine conflicting results.

ITS DNA sequence data for the two isolates of G. salmonicolor (MG597289 and MG597290/holotype), G. guanacastensis from the Bahamas and Florida and a paratype were phylogenetically
Geodina (Pezizomycetes: Wynneaceae) has a single widespread species in tropical America.

**RESULTS**

**Taxonomy**

*Geodina guanacastensis* Denison, *Mycologia* 57: 650. 1965. Figs 57–65. 1965. Figs 57–65.

**Synonym:** *Geodina salmonicolor* Angelini & Medardi, *Mycosphere* 9: 172. 2018.

**Apothecia:** 10–30 mm diam, up to (10–)25–40 mm high, terricolous, solitary or gregarious in small groups with 2–4(–6) stipitate apothecia, with shared rooting stipes, wider near the receptacle tapering downwards. **Receptacle** cyathiform to funnel-shaped, irregularly undulate at maturity, alternating smooth and hairy concentric rings, smooth areas light greyish brown (60.l.gy.Br) to light brown (57.l.Br), hairy concentric rings medium brown (58.m.Br) to dark greyish brown (62.m.Br), *Margin* differentiated, with long hairs aggregated in triangular fascicles. **Disc** smooth, light yellowish pink (28.l.yPink) to medium orange (53.m.O), strongly depressed in the centre. **Margin** composed of dark brown (59.d.Br) to deep brown (60.d.Br), walls darker and refractive, up to 1 µm thick at the apex, up to 2 µm in the lower cells; unbranched and sparsely seolate, distance between septa more than 50 µm. **Ectal excipulum** from base to flank of textura angularis *t.* prismatica, inner layer light greyish brown (60.l.gy.Br), outermost layer of the ectal excipulum from base to margin medium brown (58.m.Br) to deep brown (59.d.Br). **Ectal cells** *(7–)11–13(–16) × (5.5–)7–8(–10.5) µm at middle flank, isodiametric, wall

**Table 1.** Specimens included in phylogenetic analyses. The * indicates sequences obtained in this study from the collection listed. NA denotes not available. Collection numbers are given for taxa where a collection or DNA stock was used to generate DNA sequences.

| Taxon Name                | Collection Number | ITS   | 28S   | 18S   | RPB2  | EF     |
|---------------------------|-------------------|-------|-------|-------|-------|--------|
| *Charioacts geaster*      |                   | KC012672 | AF104340 | DQQ17609 | KC109211 |
| * Cookeina tricholoma*   | MH 686 DNA Stock  | AY945860 | AF006311 | MN103428* | MN103423* |
| *Desmazierella acicola*  |                   | AY945854 | AF104341 | DQQ17603 | LTN94774 |
| *Donadinia nigrella*     |                   | AY945853 | NA     | DQQ17592 | KC109214 |
| *Galiella rufa*          |                   | AY945850 | AF004948 | DQQ17594 | KC109213 |
| *Geodina guanacastensis* | CUP-CA 84         | MN096938* | NA     | NA     | NA     | NA     |
| * Bahama collection      |                   | MN096939* | MN096940* | MN096941* | MN103424* | MN090946* |
| *Geodina salmonicolor*   | JBSD127408        | MG597287 | NA     | NA     | NA     | NA     |
| * JBSD127409             |                   | MG597290 | NA     | NA     | NA     | NA     |
| * Gyromitra californica  |                   | AY544673 | AY544717 | DQQ470819 | DQQ471059 |
| * Komposcypha phyllogena*| DHP 10-690 DNA Stock | JQ260810 | JQ260820 | MN103430* | MN103416* |
| * Morchella elata*       |                   | U42667 | U42641 | AF107810 | HM756737 |
| * Neornula pouchetti*    |                   | AY307940 | AF104666 | DQQ17601 | NA     |
| * Phillipsia carnicolor* | DHP 7126 DNA Stock | JQ260811 | JQ260821 | MN103426* | MN100948* |
| * Pithya cupressina*     | FH 00465472       | JQ260818 | AF006316 | MN103429* | MN103415* |
| * Plectonia melastoma*   | MH 679 DNA Stock  | JX669850 | MN102128* | MN103434* | MN103422* |
| * Pseudopithyella minuscula* | Ay945849 | AF006317 | DQQ17600 | FIJ38837 |
| * Pseudoplectania nigrella* | KH.97.28 DNA Stock | AY945852 | MN096942* | MN103433* | MN103421* |
| * Pseudosarcosoma latahense* | FJ176860 | FIJ176806 | NA     | FIJ38392 |
| * Rickiella edulis*      | FH 01146895       | JQ260809 | JQ260819 | MN103425* | MN100947* |
| * Sarcosphyta austriaca* | MH 670 DNA Stock  | AY945856 | AF006318 | MN103427* | KC109210 |
| * Sarcosoma globosum*    | KH.07.04 DNA Stock | FIJ49939 | U53386 | JX943753 | KC109215 |
| * Uredula craterium*     |                   | AY945851 | AF104347 | DQQ17595 | KC109216 |
| * Wolfina aurantiopsis*  |                   | AY945859 | AF104644 | DQQ17605 | KC109212 |
| * Wynnea americana*      | FH 00445979 DNA Stock | AY945848 | MK599141 | MN103435* | MN103417* |
| * Wynnea macrospora*     | FH 00445975 DNA Stock | AY945840 | MK3535803 | MK3535793 | MN103432* | MN103419* |
| * Wynnea macrotis*       | CUP 2684 DNA Stock | MK3535804 | MK3535795 | NA     | MN103420* |
| * Wynnea sparassoides*   | FH 00445986 DNA Stock | EU360917 | MK3535796 | MN103431* | MN103418* |

GenBank accession numbers

| Taxon Name                | GenBank accession numbers |
|---------------------------|--------------------------|
| *Geodina guanacastensis*  | JBSD127408               |
| * Geodina salmonicolor*   | JBSD127409               |
| * Wynnea americana*       | JBSD127408               |
| * Wynnea macrospora*      | JBSD127409               |
| * Wynnea macrotis*        | JBSD127409               |
| * Wynnea sparassoides*    | JBSD127409               |

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slightly thickened up to *1 µm; cells at margin long rectangular, running parallel, cohering, *(16.5–)20–28.5(–30) × 2.5–3.5 µm, walls refractive and strongly thickened up to *2 µm. Medullary excipulum of textura intricata, *64–240 µm thick at flanks, cells *(14.5–)27.5–43.5(–91.5) × (3.5–)4.5–5.5 µm, thin-walled, intercellular spaces present or absent, without gel. Asci *(440–)467–536(–575) × 21.5–23(–24) µm, *(421–)425–466(–488) × 16.5–19 µm; cylindric, 8-spored, uniseriate, spars spongifera *161–192 µm, lateral walls thick, up to *3.5 µm, asci inamyloid in MLZ and LUG, with or without KOH pre-treatment, wall at apex thinner up to *2.5 µm thick, operculum eccentric, 18–9.5 µm diam; base curved and gradually tapered arising from a constricted simple septa. Ascospores *(21.7–)24–25.4(–28.3) × (11.2–)12.2–12.8(–14.5) µm, *(21.1–)23.1–24.7(–27) × (10.4–)11.3–12.1(–13.5) µm; ellipsoid, straight, inequilateral, hyaline, cyanophobic, sculptured, ornamentation consisting of coarse, irregular, longitudinal ridges (0.5–1.5 µm high) which Anastomose to form an irregular reticulum, not lost after KOH pre-treatment (spore walls sometimes loosing in KOH), with apiculi *(1.8–)3.6 µm in height; oligo- to multi-guttulate (lipid bodies), guttules pale yellow (89.p,Y), 2–3(–5) large guttules (3–6.5 µm diam.) surrounded by several smaller guttules (0.5–2.5 µm diam.), oil content inside the spores 75–90 %. Paraphyses cylindrical to slightly enlarged at the apex, apical cells *(17.5–)55.5 × 2.5–4 µm, cells below *(20–33) × 1.5–3 µm; septate, simple to bifurcate toward the base, thin-walled, with one or several yellow grey (93.yGrey) guttules in the apical cells (vacuolar bodies).

Remarks: Our description of the specimens generally agree with Dennison (1965), Angelini et al. (2018) and Ortega-López et al. (2019). We were unable to study the type material of Geodina salmonicolor from the Jardin Botanico Nacional, Dr. Rafael Ma. Moscoso (JBSB). But some differences were noted. These three authors described the length of the asci in a range between 300–450 µm, but we found the asci to be *(440–)575 µm or *(421–)488 µm. This difference may have resulted from the study of dead asci, but also asci are deeply rooted in the subhymenium often curved and twisted. It is likely that they did not measure the complete asci. Our ascospore size range agrees with Dennison (1965) and Ortega-López et al. (2019), but not with Angelini et al. (2018). In our study we noticed that some spores can swell after pre-treatment with some reagents (KOH + CR), this produces a deviation of the maximum length of the spore up to 7 µm, from 27 µm to 34 µm. This probably accounts for their measurement of spore length up to 33.5 µm. Treatment with KOH can also loosen the outer wall causing it to detach and expand several µm with respect to the inner wall. In our measurements such ascospores were excluded. Spore size was a primary feature used by Angelini et al. (2018) to distinguish G. salmonicolor. The previous reports and our observations also differ in the interpretation of the excipulum and hairs. Angelini et al. (2018) seem to have interpreted hair morphology differently and confused fasciculate hairs with single hairs, therefore their description and measures are misleading and refer mostly to fasciculate hairs not to single hairs. The medullary excipulum is described by all authors as textura intricata, but there are inconsistencies regarding the interpretation of the ectal excipulum. None of the previous reports describe the ectal excipulum at the margin, flanks and base, and clearly differences exist between the tissues in these regions (Fig. 1: E1–E2). Denison (1965) described the ectal excipulum as textura prismaticata to t. angularis, Angelini et al. (2018) noted that it was composed of t. globulosa to t. angularis and Ortega-López et al. (2019) wrote of textura angularis to t. epidermoidea. We disagree with the interpretation of these tissues as textura globulosa or t. epidermoidea. Textura angularis to t. prismaticata are found at the base (Fig. 1: E4), whereas in the margin textura porrecta to t. oblitera (Fig. 1: E3) are observed. Finally, the morphology of the ascospores is well described in all the papers, but none of them specifically mentioned the apiculi (Fig. 1: G1). Previous studies of Geodina specimens all mention that the spores have 1–2 guttules. We have observed in fresh material that ascospores are multiguttulate and that the pattern is lost when they are dead in which condition small guttules merge to form one or two large bodies (Fig. 1: G1–G2).

Molecular results

The ITS sequence of the Geodina specimen collected in the Bahamas was 100 % identical to the ITS sequence of the holotype of G. salmonicolor JBSD 127409 (GenBank # MG597290) and 99.8 % identical to G. salmonicolor JBSD 127408 (GenBank # MG597289) (Fig. 2B). The G. salmonicolor collections were determined by Angelini et al. (2018). Comparison of the ITS sequence data indicated that the three specimens of Geodina, the one from the Bahamas and the two isolates of G. salmonicolor (JBSD 127408 and JBSD 127409, Angelini et al. 2018) had respectively 99.7 %, 99.5 % and 99.6 % sequence identity to G. guanacastensis and is presented in Fig. 2B. Thus, the ITS phylogeny does not support the recognition of two Geodina species.

Phylogenetic analyses using ML and Bayesian analyses of the combined EF, 28S, RPB2, and 18S data set (Fig. 2A) indicated that Geodina formed a highly supported sister group with Wynnea species. The sister group relationship between Geodina and Wynnea was resolved in each single gene phylogenetic analyses. This relationship was furthermore supported in all single gene phylogenies, except for the EF phylogeny. The families Sarcosomataceae, Sarcoscyphaceae and Chorioactidaceae were highly supported as monophyletic in analyses of the combined data set and for individual gene analyses of the 28S, RPB2 and 18S data sets.
DISCUSSION

Our results indicate that there is a single widespread species in the genus *Geodina*. The species seems to have been collected primarily in lowland, dry tropical or subtropical forests (Denison 1965, Angelini et al. 2018, Ortega-López et al. 2019). The occurrence in these areas may account for the seeming rarity of this species since such areas may not be as frequently collected as other habitats.
Geodina and Wynnea occupy together a position on a long branch sister to members of the Sarcoscyphaceae. Molecular phylogenetic studies based on 18S and combined 28S and 18S rDNA have resolved Wynnea as an independent sister clade to the other genera of the Sarcoscyphaceae (Harrington et al. 1999, Romero et al. 2012, Angellini et al. 2018). In the current study and in Angellini et al. (2018) the Geodina collections consistently formed a highly supported sister clade with Wynnea species in the individual and combined gene analyses (Fig. 2A). Pfister in Romero et al. (2012) proposed the tribe Wynneae to accommodate Wynnea. Unlike the current analysis, which includes three species of Wynnea, this earlier analysis included only Wynnea americana. Even with this more expanded sample the long branch relationship is supported.

The species of the Wynnea and Geodina share certain morphological features (Fig. 2C). The outer excipula in both are composed of dark-walled angular cells that give rise to hairs. In Geodina the hairs are composed of adherent hyphae which form multilamellate hairs, but in Wynnea the hairs are generally separate or only loosely associated (Pfister 1979). In both cases the walls of the hairs are thick and can appear to be refractive. Ascospores of these genera are multiguttulate, and are marked with cyanophobic ornamentations. In Wynnea species the ornamentations take the form of longitudinal ridges; in G. guanacastensis the ornamentation is of robust interconnected ridges that form a reticulum, as beautifully illustrated with SEM by Ortega-López et al. (2019). The ascospores of both genera are apiculate to a greater or lesser degree. Wynnea species are characterized by forming several ear-shaped, or cup-shaped apothecia on a common stipe. The color of the hymenia of species of both genera range from pink to orange tones. Korf (1949) observed that in fresh material the color of the hymenia of W. americana was rose-pink, but in older material the hymenial color was deep purple-red. Although generally overlooked it is clear from the photograph in Ortega-López et al. (2019) that in G. guanacastensis several cupulate apothecia arise from a common stipe as in Wynnea species. These species also are found on soil. All other species of the sister family Sarcoscyphaceae are found on wood or other plant materials such as twigs, leaves and fruits. Geodina guanacastensis ascomata have been assumed to originate from buried wood. The long stalks of the ascomata show signs of having been detached from a longer structure. All photographs and specimens show signs of a broken base. Wynnea species on the other hand produce sclerotium-like structures that are composed of hyphae of the Wynnea species and hyphae and rhizomorphs of Armillaria species (Xu et al. 2019). Whether like Wynnea species, the Geodina species is associated with another fungus or whether it arises from deeply buried wood or roots remains to be demonstrated thorough and careful excavation of the ascomatal base.

Given the affinities of the species of these two genera and the phylogenetic relationships we propose to recognize this group as a family.

**Wynneaeae** Pfister & Quijada *fam. nov.* MycoBank MB833213.

*Type genus: Wynnea* Berk. & M. A. Curtis

**Diagnosis:** Ascomata medium to large with multiple apothecia arising from a common base or stalk, spathulate or cupulate, ectal excipulum of dark angular cells, thick-walled in the outer layers, giving rise to pustules and/or hairs, hairs brown thick-walled, sometimes joining to form multilamellate hairs, asci thick-walled with an eccentric, thick operculum, ascospores with two or more large guttules and several smaller one, ornamented with cyanophobic longitudinal ribs or ribs interconnecting to form a reticulum, apiculate.

Collected on soil but trophic status unknown. Wynnea is associated with Armillaria.

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**REFERENCES**

Angelini C, Medardi G, Alvarado P (2018). Contribution to the study of neotropical discomycetes: a new species of the genus Geodina (Geodina salmonicolor sp. nov.) from the Dominican Republic. *Mycosphere* 9: 169–177.

Anonymous (1976). ISCC-NBS Color-name charts illustrated with centroid colors. Inter-Society Color Council. National Bureau of Standards, Washington.

Baral HO (1992). Vital versus herbarium taxonomy: morphological differences between living and dead cells of Ascomycetes, and their taxonomic implications. *Mycotaxon* 44: 333–390.

Denison WC (1965). Central American *Pezizales*. I. A new genus of the Sarcoscyphaceae. *Mycologia* 57: 649–656.

Gardes M, Bruns TD (1993). ITS primers with enhanced specificity for basidiomycetes-application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2: 113–118.

Hansen K, LoBuglio KF, Pfister DH (2005). Evolutionary relationships of the cup-fungus genus *Pezizoides* and *Pezizoides* inferred from multiple nuclear genes: RPB2, beta-tubulin, and LSU rDNA. *Molecular Phylogenetics and Evolution* 36: 1–23.

Harrington FA, Pfister DH, Potter D, et al. (1999). Phylogenetic studies within the *Pezizales*. I. 18S rRNA sequence data and classification. *Mycologia* 91: 41–50.

Huelsenbeck JP, Ronquist F (2001). MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17: 754–755.

Korf RP (1949). *Wynnea americana*. *Mycologia* 41: 649–651.

Landvik S, Egger K, Schumacher T (1997). Toward a subordinal classification of the *Pezizales* (*Ascomycota*)-phylogenetic analyses SSU rDNA sequences. *Nordic Journal of Botany* 17: 403–418.

Miller MA, Pfeiffer W, Schwartz T (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees, In: *Proceedings of the Gateway Computing Environments Workshop* (GCE), 14 Nov. 2010, New Orleans, Louisiana: 1–8.

Moncalvo J-M, Lutzoni FM, Rehner SA, et al. (2000). Phylogenetic relationships of agaric fungi based on nuclear large subunit ribosomal DNA sequences. *Systematic Biology* 49: 278–305.

Ortega-López I, Valenzuela R, Gay González AD, et al. (2019). La familia Sarcoscyphaceae (*Pezizales, Ascomycota*) en Mexico. *Acta Botánica Mexicana* 126: e1430 (pp. 1–36).

Pfister DH (1979). A monograph of the genus *Wynnea* (*Pezizales, Sarcoscyphaceae*). *Mycologia* 71: 144–159.
Pfister DH, LoBuglio KF (2018). Lost and found: the Bermudan Donadinia seaveri found in North America, with comments on its juniper associates. *Mycologia* **110**: 215–221.

Rehner SA (2001). Primers for Elongation Factor 1-α (EF1-α). http://ocid.NACSE.ORG/research/deepphyphae/EF1primer.pdf

Rehner SA, Buckley E (2005). A Beauveria phylogeny inferred from nuclear ITS and EF1-α sequences: evidence for cryptic diversification and links to Cordyceps teleomorphs. *Mycologia* **97**: 84–98.

Romero AI, Robledo G, LoBuglio KF, et al. (2012). *Rickiella edulis* and its phylogenetic relationships within *Sarcoscyphaceae*. *Kurtziana* **37**: 79–89.

Stamatakis A (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**: 1312–1313.

White TJ, Bruns T, Lee S, et al. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR protocols: A guide to the methods and applications* (Innis MA, Gelfand DH, Sninsky JJ, et al., eds). Academic Press, USA: 315–322.

Xu F, LoBuglio KF, Pfister DH (2019). On the co-occurrence of species of Wynnea (Ascomycota, Pezizales, Sarcoscyphaceae) and Armillaria (Basidiomycota, Agaricales, Physalacriaceae). *Fungal Systematics and Evolution* **4**: 1–12.