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Coltriciella multipileata (Agaricomycetes, Hymenochaetaceae), a new species from Mexico, related to ectomycorrhizal lineages

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Abstract

Coltriciella multipileata is described here as a new species from Mexico. The species grow on soils in open areas at the vicinity of living trees of *Pinus patula*, and its known only from the Parque Recreativo Los Colomos, Jalisco. The phylogenetic analysis based on partial nuclear 28S ribosomal DNA sequences, recovered *Coltriciella multipileata* as sister group with a specimen reported as ectomycorrhizal, and closely related with other two species that are considered saprophitic. According with our preliminary analysis of character states reconstruction, the ectomycorrhizal condition appeared early in the *Coltriciella* clade, with a high rate of transitions between ectomycorrhizal and saprophitic conditions. A key for species similar to *Coltriciella multipileata* is presented.

Keywords: Hymenochaetales, Hymenochaetaceae, Polyporoid fungi, ancestral character state reconstruction, Neotropical fungi

Introduction

Coltriciella Murrill (1904: 348) is a genus in the Hymenochaetaceae that includes up to 14 species distributed worldwide (Susan *et al.* 2018). The genus is morphologically very similar to *Coltricia* Gray (1821: 644), and only can be distinguished by the presence of finely verruculose spores (Ryvarden 1991). *Coltria and Coltriciella* are recovered as a monophyletic group consistently in several independent phylogenetic analysis (Larsson *et al.* 2006, Tedersoo *et al.* 2007a, Valenzuela *et al.* 2012, Bian & Dai 2015, 2017), but the limit between both genera is less clear. Some studies recover *Coltriciella* as a monophyletic group (i.e. Larsson *et al.* 2006, Valenzuela *et al.* 2012), while some other recover it as a paraphyletic grade (Susan *et al.* 2018), because of the placement of *Coltriciella globosa* L.S. Bian & Y.C. Dai. (2014 [2015]: 194).

In Mexico, three species of *Coltriciella* have been recorded: *C. dependens* (Berkeley & Curtis 1853: 431) Murrill (1904: 348), (Vásquez & Guzmán-Dávalos 1991; Romero-Bautista *et al.* 2010), *C. oblectabilis* (Lloyd 1912: 164) Kotlaba, Pouzar & Ryvarden (1984: 140) (Raymundo & Valenzuela 2003), and *C. sonorensis* R. Valenz., Esqueda & Decock, in Valenzuela *et al.* (2010: 184) described from Mexico and only known from the state of Sonora (Valenzuela *et al.* 2012).

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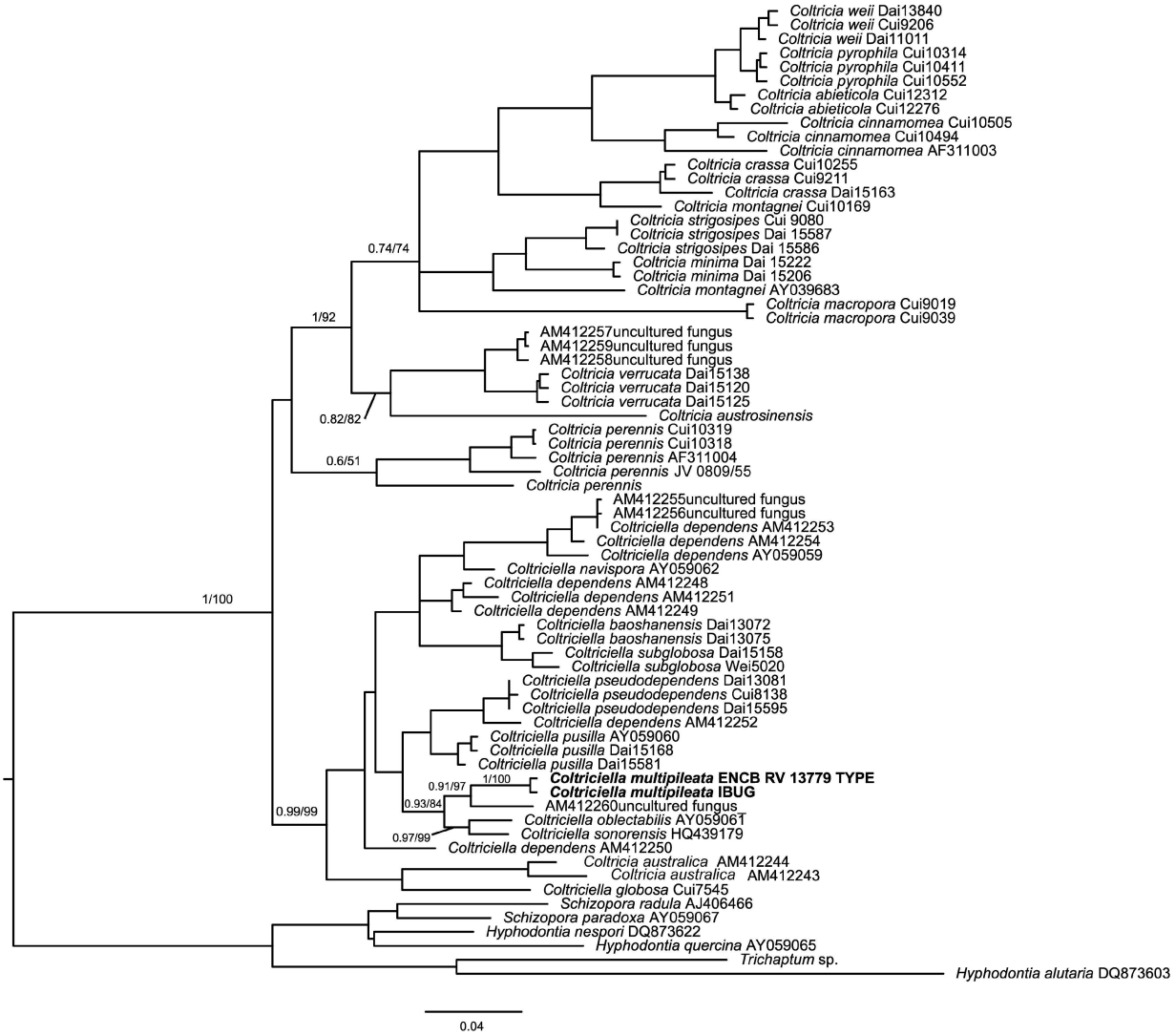

FIGURE 1. Majority rule consensus tree form the Bayesian inference analysis of the nLSU. All the branches have a posterior probability above 0.95, and bootstrap frequencies of 95%, except when it is indicated otherwise.

The new species was collected in the vicinity of *Pinus patula* trees, and it is assumed to be a saprophytic species. But, because the ectomycorrhizal nutritional mode had been previously reported in *Coltricia* and *Coltriciella* (Danielson 1984, Tedersoo *et al.* 2007a), we decided to perform an exploratory analysis of ancestral character states reconstruction, to assess the number of independent origins for the mycorrhizal habit, and to estimate the likelihood of an ectomycorrhizal ancestor for the new species.

In this contribution, our main goal is to describe a new species collected from the state of Jalisco in Mexico, providing a detailed description on its morphology, a molecular characterization and a taxonomic key for distinguish the new species from similar ones.

Materials and methods

Study Area:—The specimens examined were collected on soils in open areas near *Pinus patula*, in a forests patch at Parque Recreativo Los Colomos, Guadalajara, state of Jalisco, Mexico. The Park is a protected area (92 ha) with recreational, sport and cultural activities, which is intensively visited, mainly because it is located in the downtown area.

FIGURE 2. Basidiocarps and microscopic structures of *Coltriciella multipileata*. A–C: Basidiome multipileate with branched stipite in R. Valenzuela 13779. D: Pore surface in R. Valenzuela 13779. E: Basidiome in V. Iñiguez Mejía 42. F–G: Hymenium and subhymenium. I–J: basidia and basidiospores (optical microscope). H and K: basidiospores (Scanning Electronic Microscope). Scale bars: **a** 10mm; **b**, **c** 5mm; **d** 1mm; **e** 100µm; **f**, **g**, **i**, **j**, **k** 1µm; **h** 10µm.

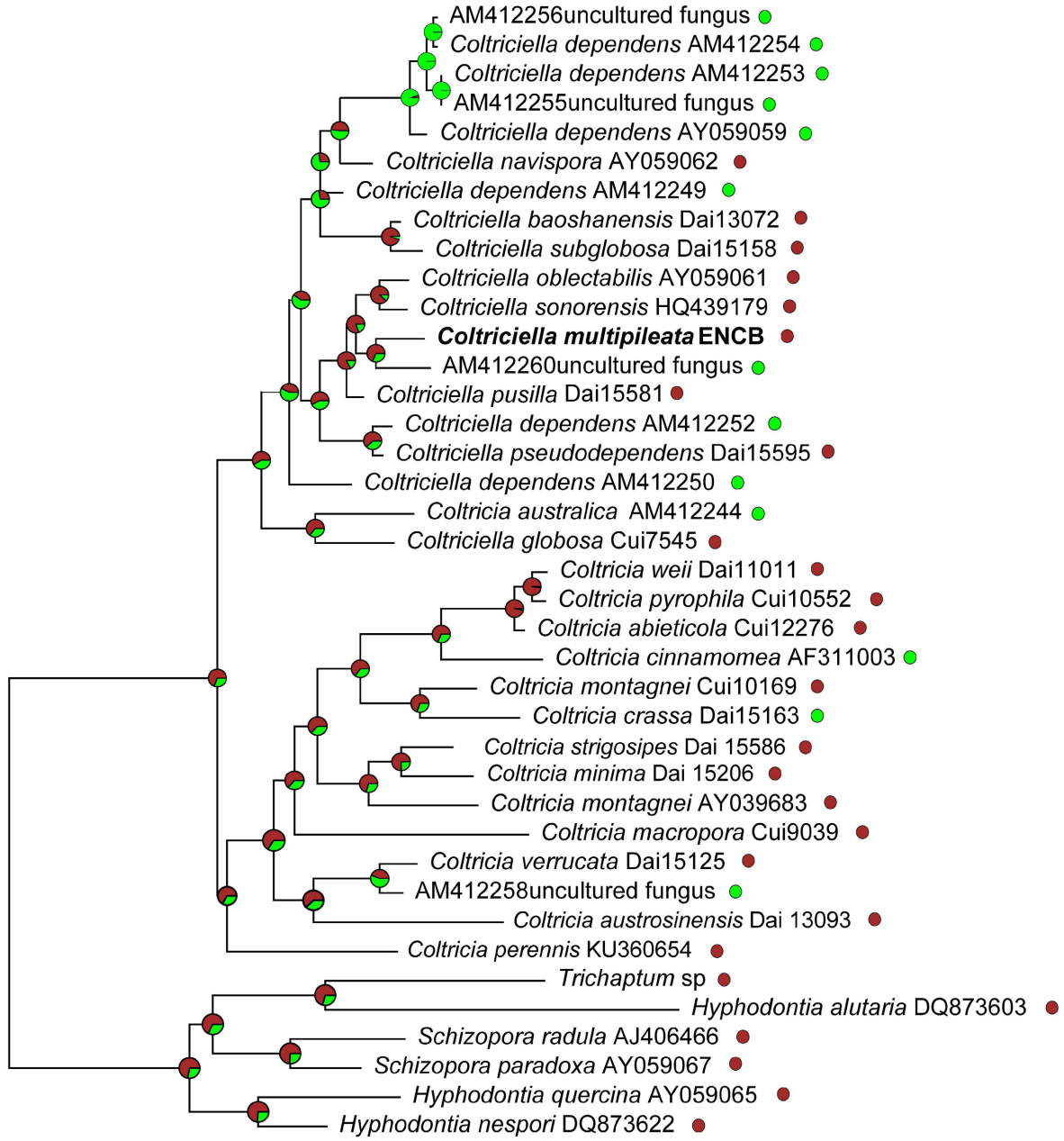

FIGURE 3. Ancestral character state reconstruction for the ectomycorrhizal condition, using maximum likelihood criteria. In the pie chart on each node, green color represents ectomycorrhizal condition and brown color represents saprophytic condition.

Morphological analyses:—Macro- and micro-morphological analyses were conducted using protocols outlined by Ryvarden (1991) and Cifuentes *et al.* (1986). Basidiome colours were described in dried specimens following Kornerup & Wanscher (1981). Measurements of micro-morphological characters were taken from rehydrated tissues in 5% aqueous KOH, while amyloid/dextrinoid reactions were taken with Melzer's reagent in a Zeiss Axiolab microscope. Voucher specimens were deposited in ENCB and IBUG herbaria with duplicates in MUCL Herbarium (acronyms according to Thiers B. [continuously updated]).

DNA extraction, amplification, and sequencing:—We performed extraction of total DNA and amplification of the nuclear ribosomal 5′ end of the LSU as described in Decock *et al.* (2007). The primers LR0R and LR5 (Vilgalys & Hester 1990, Cubeta *et al.* 1991) were used for PCR amplifications. Successful PCR reactions resulted in a single band observed on an 0.8% agarose gel, corresponding to approximately 850–900 bp. Sequencing reactions were performed using CEQ DTCS Quick Start Kit® (Beckman Coulter), according to the manufacturer's recommendations, with the primers LR0R, LR3, LR3R, LR5 (http://biology.duke.edu/fungi/mycolab/primers.htm).

Phylogenetic analyses:—We used the taxonomic sampling and alignment from Bian *et al.* (2016), which included the ITS and nLSU regions, as starting point (www.treebase.org, study ID 18687). Because we were only able to obtain nLSU region, we used only nLSU sequences for the phylogenetic analyses. For the outgroups selection we followed Bian *et al.* (2016). Six sequences of ectomycorrhizal *Coltricia* and *Coltriciella* species (accessions AM412255-60) from Tedersoo *et al.* (2007a) were added manually in Mesquite 3.31 (Maddison & Maddison 2017), and two sequences representing the new species were added manually (MH487727-8). A total of seventy sequences were included.

We performed a phylogenetic analysis with Bayesian inference in MrBayes 3.2.6 (Ronquist *et al.* 2012) using the CIPRES platform (Miller *et al.* 2015). Nucleotide substitutions for each partition was modeled using a reversible jump MCMC approach (Huelsenbeck *et al.* 2004) and character rate variation was modeled using gamma distribution with four categories. We ran a MCMCMC for 10 million generations in two independent sets of four chains each, sampling every 1000 steps, burnin was set to 25%, convergence, mixing and effective sample size for the parameters were monitored in Tracer 1.7.1 (Rambaut *et al.* 2018). After a first round of analysis, we decided to reduce the temperature parameter (temp= 0.01), in order to improve mixing as sugested in MrBayes documentation. Character support values were estimated with a non-parametric bootstrap (Felsenstein 1985) in IQ-TREE 1.6.9 (Nguyen *et al.* 2015). We performed a model selection search in IQ-TREE, and the best model found for our alignment according with Akaike information content (GTR+F+R3) was used for the bootstrap analysis with 1000 replicates; bootstrap values were drawn on the maximum clade credibility tree found in the Bayesian inference search, as recommended elsewhere (García-Sandoval 2014).

Species delimitation:—The present analysis includes sequences for the nLSU only, and even considering that species in the genus have been described using only nLSU (i.e. Bian & Dai 2015), we decided to provide additional support for the delimitation of the new species using a Bayesian model for species delimitation (Poisson tree process model, Zhang *et al.* 2013). Phylogenetically explicit models for species delimitation are particularly informative when only one molecular marker is available, and outperforms some other non-phylogenetic criteria (i.e. similarity percentage, Dellicour & Flot 2015). Even when is not widely used for describing fungal species, nowadays the mycological community is more aware of the benefits of using this approach (Hibbett *et al.* 2016). We applied this model over the maximum clade credibility tree, recovered from the trees sampled in the Bayesian inference analysis, using Tree Anotator 1.8.4. The model was applied in the web server (http://species.h-its.org/) using Bayesian inference frame. A MCMC chain was set with 500,000 generations with 10% burnin; convergence, mixing, and effective sample size were monitored in Tracer 1.7.1 (Rambaut *et al.* 2018).

Ectomycorrhizal evolution:—The ancestral character reconstruction analysis was performed over the maximum clade credibility tree, selected from the Bayesian analysis trees sample. We coded nutritional mode either as ectomycorrhizal or saprophytic following literature records (Danielson 1984, Tedersoo *et al.* 2007a, b). We coded a terminal as ectomycorrhizal if correspond to a species that were explicitly documented as such, or if the specimen was documented as ectomycorrhizal even if the species identity was not determined, as it was the case for specimens collected in Seychelles (Tedersoo *et al.* 2007a). The other terminals were coded as saprophytic because it is the assumed condition in the genus. We estimate ancestral states probabilities for the internal nodes with a maximum likelihood method (Pagel 1994). The analysis was performed in R (R Core Team 2020) using the function "ace" in package Phytools (Revell 2012).

Results

Phylogenetic analysis:—After 10 million generations, the average standard deviation between chains was of 0.004. The convergence between both chains and mixing were inspected in the output with Tracer 1.7.1 (Rambaut *et al.* 2018). Chain swapping values in MrBayes were between 0.41 and 0.54 and effective sample size (ESS) for all the parameters was 283 or higher.

Overall topology is highly congruent with those recovered in previous studies (Bian *et al.* 2016, Tedersoo *et al.* 2007a). *Coltriciella* is recovered as a monophyletic group with high support, but representatives of *Coltricia australica* L.W. Zhou, Tedersoo & Y.C. Dai, in Zhou & Tedersoo (2012: 124) were recovered as sister group with *Coltriciella globosa* (Fig. 2), at the most basal part of *Coltriciella* clade, this result is consistent with previous reports (Tedersoo *et al.* 2007a, Zhou & Tedersoo 2012, Bian & Dai 2014).

Coltricia multipileata was recovered in an American clade, altogether with *C. oblectabilis* and *C. sonorensis*; besides, *C. multipileata*, *C. oblectabilis* and *C. sonorensis* grouped with an unnamed ectomycorrhizal lineage.

On the other hand, *Coltricia* is recovered as a monophyletic group, with the exception of the position of *C. australica*, which were recovered in the *Coltriciella* clade, as mentioned above.

Species delimitation and ectomycorrhizal evolution:—Results from Bayesian model for species delimitation were manually inspected, convergence, mixing and effective sample size (ESS) of the MCMC in Tracer 1.7.1; ESS for the model was 795. The *Coltriciella multipileata* clade was recovered as a single species with a posterior probability of 0.93 (Supplement 1).

Ancestral character states reconstruction using maximum likelihood, estimate a saprophytic habit for the most recent common ancestor (MRCA) of the *Coltricia-Coltriciella* clade (0.69), as well as for the MRCA in *Cotricia* (0.66) and *Coltriciella* (0.58). The MRCA of the clade in *Coltriciella* that excludes *C. globosa* is inferred with ectomycorrhizal habit (0.57), and three subsequent reversals to saprophytic habit are inferred in the *Coltriciella* clade, and *C. multipileata* is recovered in a large clade inferred as saprophytic (Fig. 3).

Taxonomy

Coltriciella multipileata R. Valenz., Raymundo, Decock & R. García-Sandoval *sp. nov.*
Figs. 2A–2K
MycoBank: MB 826758

Basidiomata annua, stipitata, multipileata. Pileus 6–12 mm latus, imbricatus, petaloideus vel spathulatus, flavo-brunneus vel brunneus, zonatus tenues, striatus. Hymenophorum porosum, poris irregularis vel elongatis, (1–) 2–3 per mm. Stipites laterales, rameales, brunnei, tomentoses.Systema hypharum monomiticum, hyphis generatoriis septis simplicibus. Basidiosporae (7.2–) 7.6–9 (–9.6) × (4–) 4.5–5.6 µm, oblongae vel ellipsoidae, in proportione minore cylindricae, pallide flavo-brunneae vel rubro-brunneae, nonamyloideae, verrucosae, crassitunicatae.

Holotype. MEXICO, JALISCO STATE: Municipality of Guadalajara, Parque Recreativo Los Colomos, 1500 masl., ad terram in sylvis *Pinus patula*, 25 September 2009, R. Valenzuela 13779, (Holotypus ENCB, Isotypus MUCL). DNA sequences: MH487727 (nucLSU).

Etymology. *Multipileata* (latin): referring to basidiome with many pilei in a unique and basal stipe.

Basidiome annual, stipitate, entire structure 30 mm high and 25 mm wide, coriaceous texture, brittle or fragile when dry; **stipe** lateral and branched, giving rise to numerous small pilei, flattened to cylindrical, tapering to the apex, 15–20 mm long and 0.5–2 mm diam., rusty brown (6E8) to brown (7E8), velutinate to tomentose, with a granulate base consisting of organic matter, soil and mycelium; **pilei** imbricate, petaloid to spathulate, 6–12 mm wide and 3 mm thick, light brown (6D8), rusty brown (6E8) to brown (7E8), finely tomentose to fibrillose, radially striate and striate-cracked toward the margin with flattened bundles of hyphae, projecting free before margin edge, weakly zonate; margin thin, partly incised, deflexed when dry, wavy; **pore surface** light brown (6D8) to rusty brown (6E8), with the edges yellowish; **pores** rounded, elongate or irregular shaped, entire to fimbriate, (1–) 2–3 per mm (radially measured), with tomentose and thick dissepiments; **tubes** up to 2 mm deep, concolorous with the pores surface; **context** very thin, less than 1 mm thick, homogeneous, light brown (6D8), fibrous.

Hyphal system monomitic; **generative hyphae** simple septate, unbranched to branched, with many bifurcate hyphae, thin- to thick-walled, golden yellow to reddish brown in KOH, negative in Melzer's reagent; **hymenophoral trama** with hyphae of the 4–7.2 µm diam., interwoven, golden yellow to yellowish brown in KOH, simple to bifurcated, thick-walled; **contextual hyphae** sub-parallel to slightly interwoven, yellowish brown to reddish brown in KOH, simple to branched, mainly bifurcate near of hymenophoral trama, thick-walled, 4–7.2 µm diam.; **pileipellis** a cutis, up to 50 µm thick, hyphae 3–5 µm diam., prostrate, parallel to sub-parallel, hyaline, yellowish to yellowish brown in KOH, simple to scarcely branched, thick-walled; **stipe hyphae** parallel to sub-parallel, yellowish brown to reddish brown in KOH, simple to scarcely branched, some bifurcated, thick-walled, 4–6.4 µm diam.; **stipitipellis** a trichoderm, 400 µm thick, up to 650 µm thick in some parts, hyphae 4.5–8 µm diam., erect, semi-erect, laxly interwoven, reddish brown to brown in KOH, simple to branched, some bifurcate, thick walled; **subhymenium** very developed, up to 48 µm thick, ramose to ramose-inflated, with two layers, one near the trama, laxly, pale brown, with bifurcated hyphae, 4–7.2 µm diam., yellowish to pale brown in KOH, thin- to thick-walled; another near the hymenial layer, compacted, brown, with inflated hyphae and cells, some bifurcated, 5.6–8.8 µm diam., pale brown to reddish brown in KOH, thin to thick-walled; **basidia** clavate, hyaline in KOH, base simple septate, 19.4–23.4 × 7–8.3 µm, with 4 sterigmata, 5.1–

6.4 µm long; **basidiospores** oblong to ellipsoid, some cylindrical, attenuated towards the apex, pale yellowish brown, rust brown to reddish brown in KOH, inamyloid, finely verrucose in optical microscope, and mostly unconnected ridges and some warts more or less arranged in lines and sometimes forming subreticulated ridges on some parts of the spore in MEB, thick walled (up to 1.0 µm), uniguttulate, (7.2–) 7.6–9 (–9.6) × (4–) 4.5–5.6 µm [ave= 8.3 × 4.8 µm; Q= (1.45–) 1.56–1.92 (–2.0) µm, aveq= 1.71 µm]; cystidia and other sterile hymenial elements absent.

Ecology, range, and distribution. Solitary, growing on soil in open areas, in the vicinity of living *Pinus patula* trees, in the Parque Recreativo Los Colomos. Know only from the type locality in Jalisco.

Additional studied specimen: MEXICO, JALISCO STATE: Municipality of Guadalajara, Recreation Park Los Colomos, 1500 masl., ad terram in sylvis *Pinus patula*, 19 September 2008, *V. Iñiguez-Mejía 42* (IBUG, duplicates in ENCB). DNA sequences: MH487728 (nucLSU).

Key to selected species of *Coltriciella*

1. Basidiome resupinate to effuse-reflexed ..... 2.
– Basidiome stipito-pileate ..... 3.
2. Basidiome resupinate ..... *C. tasmanica*
– Basidiome effuse-reflexed ..... *C. corticicola*
3. Stipe branched, giving rise to many small petaloid to spathulate pilei ..... *C. multipileata*
– Stipe unbranched, giving rise to one pileus ..... 4.
4. Basidiome pendant ..... *C. dependens*
– Basidiome erected, pleuropodal or mesopodal ..... 5.
5. Basidiome mesopodal ..... 6.
– Basidiome pleuropodal ..... 7.
6. Basidiospores broadly ellipsoid, 6–8 × 5–6.5 µm ..... *C. subpicta*
– Basidiospores oblong ellipsoid with rounded base and somewhat tapering at the other end, 7–10 × 4–5 µm ..... *C. oblectabilis*
7. Basidiospores navicular, 10–12 × 4–5 µm ..... *C. navispora*
– Spores less 10 µm long 7
8. Pores regular, 2–4 per mm ..... *C. pusilla*
– Pores rounded, elongated to daedaloid, 2–3 per mm ..... *C. sonorensis*

Discussion

Our results recover *Coltriciella* clade with high support (Fig. 1), but two representatives of *Coltricia australica* are recovered at the base of the group in a clade with *Coltriciella globosa.* Our result is congruent with previous ones (Tedersoo *et al.* 2007a, Bian & Dai 2015). The specimens from *Coltricia australica* initially were identified as *C. cinnamomea,* and included as such in the phylogeny reported by Tedersoo *et al.* (2007a), where the specimens were recovered at the base of a clade that included all the *Coltriciella* species sampled. Latter on Zhou & Tedersoo (2012) formally describe *Coltricia australica*, making reference to the previous phylogenetic results (e.g. Tedersoo *et al.* 2007a), but without including any new phylogeny. Few years later Bian & Dai (2015) described *Coltriciella globosa*, and their phylogeny recovered the new species as sister group with *Cotricia australica*, at the base of a clade that included all the specimens of *Coltriciella*, but the rest of *Coltricia* species sampled were recovered as paraphyletic.

Coltricia australica bears smooth spores, which is the character considered diagnostic for the genus, and *Coltriciella globosa* also exhibit the diagnostic character for its genus (ornamented spores). If *Coltricia australica* is included in *Coltriciella*, the new combination will blur the morphological boundaries between both taxa, and even when both genera will remain monophyletic, *Coltricia* is recovered with no support, and considering previous results (Bian & Dai 2016) where the genus is recovered paraphyletic, chances are high that will end in the unwanted situation where both genera are not reciprocally monophyletic (Vellinga *et al.* 2015).

All things considered, at this moment we don't have enough solid evidence for make a new combination that will blur the boundaries between both genera. Also we consider that such taxonomic change needs to be supported on more than one single locus. It has been reported that the amplification of the ITS region is complicated in these two genera (Zhou & Tedersoo 2012), and our experience corroborate it. We consider that will be more cautious to produce a more suitable data set, rather than hurry the nomenclatural changes.

On the other hand, the representatives of *Coltriciella multipileata* are recovered in a monophyletic group, with high support (Fig. 1). Also the Bayesian model for species delimitation recovers the species with a high posterior probability (0.93), the new species is the one with the highest posterior probability in the *Coltriciella* clade according with our

results (supplementary figure 1). We decided to apply this Bayesian method for species delimitation because we were able to produce only one molecular marker, this practice is not so common in fungal taxonomy, but we consider that it provide additional evidence that can be easily incorporated in regular species descriptions when only one marker is available, as suggested somewhere else (Hibbett *et al.* 2016). Methods for species delimitation based on phylogenetic trees have been reported sensitive to mutation rates (Dellicour & Flot 2018), with a tendency to over-split lineages at high mutation rates, and over lumping at low rates, both situations are observed in our results. On simulations, best performance for the bPTP method was observed when population sizes was small (Dellicour & Flot 2018). *Coltriciella multipileata* is a species only known from a single locality, and this may correspond to the mentioned condition, on the other hand species with very large distribution as *C dependens* are neither recovered as monophyletic or as a single species.

Additionally to phylogenetic evidence, morphological evidence for the new species is also abundant. The new species can be recognize because its multipileate and pleuropodal basidiome with branched stipe giving rise to many petaloid to spathulate pilei, the irregular, rounded to elongated pores, and the basidiospores features characterize this species. It can be compared to *C. oblectabilis* and *C. dependens*, occurring also in Mexico (Raymundo & Valenzuela 2003; Vásquez & Guzmán-Dávalos 1991). *Coltriciella oblectabilis* is easily distinguished by its unipileate mesopodal basidiomes and infundibuliform pilei (Gilbertson & Ryvarden 1986). *Coltriciella dependens* differs in having pendant basidiomes, attached by a small unbranched stipe at the vertex.

Coltriciella navispora T.W. Henkel, Aime & Ryvarden in Aime *et al.* (2003: 617), *Coltriciella pusilla* (Imazeki & Kobayasi 1966: 42) Corner (1991: 50) and *C. sonorensis* also have pleuropodal basidiomes, but they are simple or unbranched stipes, also differing in the shape and size of the spores. The first has larger and cylindrical basidiospores, the second has smaller and ellipsoid basidiospores and the last oblong to cylindrical basidiospores. Phylogenetically, *C. navispora* and *C. pusilla* are also distantly related to the *Coltriciella multipileata* samples, but they have different ecological requirements: *C. navispora* was found growing in hollowed, well-decorticated trees or in the underside of fallen trunks in forests dominated by *Dicymbe corymbosa* Spruce ex Benth. in Guyana and *C. pusilla* grown on the rotten stumps of *Castanopsis* (Fagaceae) in eastern Asia, while *C. multipileata* was also found on soil in a *Pinus patula* forest in Mexico.

Ectomycorrhizal evolution:—Our analysis should be considered preliminary as long as taxonomic sampling was oriented to investigate relationships of the new species inside the *Coltriciella* clade. Following our first results, and considering the affinity of the new species with the ectomycorrhizal lineage, we decide to investigate the evolutionary pattern of this nutritional mode, with emphasis in the clade containing *Coltriciella multipielata*.

According with our results, *Coltriciella* had an early acquisition of the ectomychorrhizal (ECM) habit, with a later reversals to the saprophytic habit and two reversals to ECM condition (Fig. 3). In *Coltricia* the saprophytic condition is constant from the beginning, with at least three independents transitions to the ECM habit. This pattern of frequent switches between ectomychorrhizal and saprophytic conditions may be indicative of high instability the nutritional mode.

Recently, it has been documented a dual ecology in several species of Agaricomycotina, where some soil saprotrophs can behave as ectomycorrhizal as well (Selosse *et al.* 2018). This dual capacity has been documented in other species of Hymenochaetaceae (Smith *et al.* 2017), but not yet in *Coltricia* or *Coltriciella*. The presence of a dual ecology in the *Coltricia-Coltriciella* clade may explain the apparent instability, and high transition rate, in the nutritional modes, but additional information in the biology of the species is needed before we can provide some explanation for the pattern.

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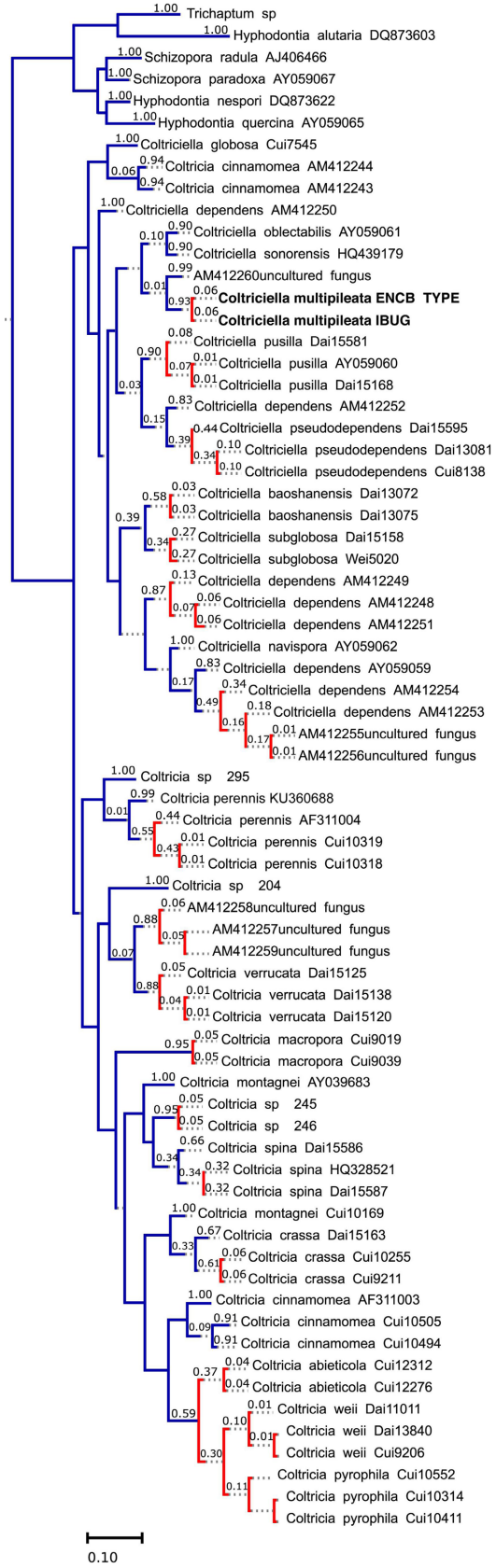

SUPPLEMENTARY FIGURE 1. Tree obtained from the bPTP analysis. Clades in red represent single species, as well as terminal branches in blue. Numbers next to branches represents Posterior Probabilities for the species hypotheses.