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ORIGINAL ARTICLE

Tomentella brunneoincrustata, the first described species of the Pisonieae-associated Neotropical *Tomentella* clade, and phylogenetic analysis of the genus in Mexico

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Abstract The /tomentella-thelephora lineage is one of the most highly dominant clades among ectomycorrhizal communities worldwide. Despite its importance as a root symbiont, its fruit bodies are inconspicuous and rarely found. Knowledge regarding the diversity of *Tomentella* in the Neotropics is scarce, and is based largely on environmental samples. Here, we describe a new species, *Tomentella brunneoincrustata*, including its basidiocarp morphology, mycorrhizal anatomy, and ecology. Because knowledge of *Tomentella* in Mexico is scarce, we provide the first phylogenetic analysis of this genus in the country. We sequenced the nrITS region of the fungal samples, and sequenced the *rbcL* and *trnL* regions to identify the host plant. The phylogenetic analyses were conducted by Bayesian inference. The Bayesian analysis showed that several paraphyletic clades within the lineage /tomentella-thelephora are associated with Pisonieae present across tropical regions of the world. However, the ectomycorrhizae sequences from Puerto Rico, Florida, Dominica, and Mexico constituted a well-supported monophyletic clade that we denote as the "Pisonieae-associated Neotropical *Tomentella* clade". Within this clade, *T. brunneoincrustata* was characterized as follows: a thin crustose, strongly attached to the substrate basidiome; concolorous subiculum, undifferentiated and sterile margin; two types of subiculum hyphae; and small (<8 μm) globose to ellipsoid spores. This species develops in tropical dry forests, where it associates with hosts in the Pisonieae tribe within the Nyctaginaceae. The remaining *Tomentella* fruit body vouchers collected in temperate forests of Mexico belonged to clades related to *T. atramentaria, T. pilosa, T. muricata, T. fuscocinerea, T. stuposa, T. punicea, T. atroarenicolor, T. bryophila, and T. lateritia*. Five fruit body vouchers had unique sequences forming independent and unknown clades of *Tomentella*.

Keywords Ectomycorrhizal · Neotropics · Pisonieae · Phylogeny · *Tomentella* · Tropical dry forest

Introduction

The Thelephoraceae family comprises the genera *Amaurodon, Thelephora, Pseudotomentella, Tomentella* (Larsson et al. 2004; Agerer 2006), and *Odontia* (Tedersoo et al. 2014). This family presents clavarioid, effused, flabelliform, pileate or resupinate basidiocarps (Agerer 2006). A characteristic apomorphy of the family is the irregular-shaped, non-amyloid,

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ornamented, and often dark basidiospore with a large apiculus (Larsson et al. 2004). *Tomentella* has inconspicuous resupinate fruit bodies formed by several layers of loose hyphae on soil, wood, twigs or rock surfaces (Kõljalg 1996). This genus is paraphyletic, and it comprises species that are divided into two lineages: an ectomycorrhizal (/tomentella-thelephora) and a saprotrophic (*Tomentella* p. parte) lineage. The /tomentella-thelephora lineage has a pan-global distribution and is one of the most species-rich and abundant ectomycorrhizal (ECM) clades associated with all major plant host taxa in a variety of ecosystems (Tedersoo et al. 2010a). The mycorrhizae of *Tomentella* are morphologically diverse (Jakucs et al. 2015), but share more than three of the following features: black-brown to brown mycorrhiza; clamped hyphae; an angular outer mantle layer; mantle cells that are organized in a star-like pattern; a mantle surface network composed of hyphae or angular-triangular, horn-shaped cells; groups of globular cells on the mantle surface; rhizomorphs with bilateral, nodal ramifications and a rind formed by thin, clamped, densely entwined, multi-branched marginal hyphae; and clamped cystidia (Jakucs and Erõs-Honti, 2008).

The /tomentella-thelephora lineage has the following biological and ecological traits. In almost any ECM fungal community (based on mycorrhizal DNA), it is among the three most dominant groups, based on either the number of MOTUs (molecular operational taxonomical units) or the frequency of its DNA sequences (e.g. Dahlberg et al. 1997; Kõljalg et al. 2001; Trowbridge and Jumpponen 2004; Haug et al. 2005; Peay et al. 2007; Smith et al. 2007; Morris et al. 2008; Hynes et al. 2010; Suvi et al. 2010; Tedersoo et al. 2010b; Smith et al. 2011; Bonito et al. 2012; Brown et al. 2013; Wu et al. 2013). Despite its importance as a root symbiont, its fruit bodies are inconspicuous and rarely found (Jakucs and Erõs-Honti, 2008; Bâ et al. 2012). Most of the lineage appears to be ECM (Tedersoo et al. 2010a), while its sister genus *Odontia* has a stable isotope pattern with an intermediate position between ECM fungi and saprotrophs. The ^{13}C pattern of this genus suggests that it does not obtain carbon from its fruiting substratum, although its C source is unknown (Tedersoo et al. 2014). As a consequence of the morphological plasticity of their ectomycorrhizae, the species of /tomentella-thelephora can be distributed either in the mineral soil horizon (Harrington and Mitchell 2005; Baier et al. 2006) developing a “contact exploration type” ECM, or in the organic horizon of broad-leaved forests (Tedersoo et al. 2003), in which they are often attached to plant foliar debris. In the latter case, they develop slightly or highly differentiated rhizomorphs, indicating that these morphotypes belong to the “medium-distance exploration type” (Jakucs and Erõs-Honti, 2008).

While the /tomentella-thelephora is dominant in boreal and temperate forests in the Northern Hemisphere, it has also been identified in the Southern Hemisphere and in tropical and subtropical ecosystems such as those in India (Thind and Rattan 1971), Korea (Jung 1994), and the Canary Islands (Larsen 1994). It was recently found to be dominant in the following tropical areas: subtropical broadleaf mixed forests in China (Gao et al. 2015); *Coccoloba uvifera* coastal forests in the Guadeloupe island in the Lesser Antilles (Séne et al. 2015); African tropical forests containing Caesalpinioideae (Fabaceae), Sarcolaenaceae, Dipterocarpaceae, Asteropeiaceae, Phyllanthaceae, Sapotaceae, Papilionoideae (Fabaceae), Gnetaceae and Proteaceae, distributed in open, gallery and rainforests of the Guineo-Congolian basin; Zambezian Miombo woodlands of East and South-Central Africa; and Sudanian savanna woodlands of the sub-Saharan region (Bâ et al. 2012).

Despite their importance in tropical ecosystems, most *Tomentella* species have been identified in temperate regions (Larsen 1974, Jülich and Stalpers 1980, Stalpers 1993, Kõljalg 1996). Several new tropical species were recently described from Africa (Yorou et al. 2007; Yorou and Agerer 2007; Yorou and Agerer 2008; Yorou et al. 2011; Yorou et al. 2012a; Yorou et al. 2012b) and the Seychelles (Suvi et al. 2010). However, knowledge regarding the diversity of *Tomentella* in the Neotropics is scarce, and based only on environmental samples from Ecuador (Tedersoo et al. 2010b), Dominica, Puerto Rico, and Vieques (Hayward and Horton 2014). Similar to those from other regions worldwide, environmental DNA sequences in the Mexican Neotropics indicate that the /tomentella-thelephora lineage is dominant in the ECM roots of several ecosystems including subtropical pine-oak forests (Garibay-Orijel 2008), cloud oak forests (Morris et al. 2009), alpine conifer forests (Reverchon et al. 2010), and *Alnus* temperate and tropical forests (Kennedy et al. 2011). However, based on basidiocarp collections, only *T. chlorine* (Massee) G. Cunn., *T. ferruginea* (Pers.) Pat., *T. griseoumbrina* Litsch., *T. pilosa* (Burt) Bourdot & Galzin, *T. subsaccicola* M.J. Larsen, and *T. umbrinospora* M.J. Larsen have been detected in Mexico (Welden et al. 1979; Urbizu et al. 2004; Contreras-Pacheco 2008; Contreras-Pacheco et al. 2014).

In our laboratory, we study the diversity, ecology, and associations of ECM fungi residing in Neotropical dry forests along the Pacific coast of Mexico. In this seasonal ecosystem, the /tomentella-thelephora lineage has been shown to be dominant in the ECM community, consisting of species new to science (Ramírez-López et al. 2015). Here, we describe a new species, *Tomentella brunneoincrustata,* including its basidiocarp morphology, mycorrhizal anatomy, ecology, and host associations. Because knowledge regarding *Tomentella* in Mexico is scarce, we also provide the first phylogenetic analysis of the diversity of this genus in this country.

Materials and methods

Study site The study was conducted at the Chamela-Cuixmala Biosphere Reserve (N 19°30’, W 105°03’) in

Jalisco, Mexico (Fig. 1), where the principal type of vegetation is tropical dry forest, and the tropical sub-deciduous forest is restricted to creeks and streams. During the summer, the weather is sub-humid and warm, whereas it is dry in the winter. The tropical dry forest exhibits water stress for 8 months, and the rainy season usually extends from July to October, which coincides with hurricane season. The average annual precipitation is 784.8 mm (1977–2011), and the average annual temperature is 24.6 °C, with an average maximum and minimum of 30.3 °C and 19.5 °C, respectively. The atmospheric humidity is >65 % during the rainy season (Bullock 1986; García-Oliva et al. 1995).

Sampling The reserve was accessed during the rainy season each year from 2012 through 2014, and opportunistic sporocarp sampling of ectomycorrhizal species was conducted according to O'Dell et al. (2004). Root tips were sampled with soil cores (PVC tubes 30 × 5 cm; ~589 cm^3 of soil) under suspected ectomycorrhizal hosts. The ECM were separated from the roots by carefully washing of the soil with tap water into a sieve. All the ECM were then isolated using a stereomicroscope. The ECM were fixed in 96 % ethanol and stored at 4 °C for a maximum of 2 weeks until further processing. All of the morphotypes were photographed prior to the anatomical analysis. The root tips were mounted in Paraplast (Leica Biosystems, Buffalo Grove, IL, USA); the anatomical slices were performed with a rotation microtome, and then mounted and stained in permanent preparations according to Sandoval-Zapotitla (2005). The ECM morphotypes were described after fixation, based on morphological and anatomical characteristics according to Agerer and Rambold (2004–2015).

Morphological data The macroscopic characteristics of the sporocarps were determined based on fresh material, and the color was determined according to the Munsell soil color charts (Munsell Color Company 1954). The microscopic characteristics of the fruit body vouchers were observed using tissue rehydrated in 2.5 % KOH by Nomarski Interference Contrast with an Olympus BX51 microscope. All of the measurements of basidia ($n = 10$), basidiospores ($n = 30$), and hyphae ($n = 30$) were performed using 1000× KOH preparations. We calculated the length/width ratio (Q), average ($\underline{Q}$), average length ($\underline{L}$) and average width ($\underline{W}$) of the spores. The spore ornamentation was observed using a scanning electron microscope (JEOL JSM-5310LV).

Molecular procedures When sufficient material was collected from a given ECM morphotype, a 1–2 mm section was used to extract DNA with the XNAP kit (Sigma-Aldrich Corp., St. Louis, MO, USA). DNA was extracted from the sporocarps using the same protocol as that used for the ECM. We amplified the nuclear ribosomal internal transcribed spacer (nrITS) region by polymerase chain reaction (PCR) with the ITS1F/ITS4 primer pair (Gardes and Bruns 1993) using RubyTaq PCR Master Mix (Affymetrix, Inc., Santa Clara, CA, USA). DNA extraction and PCR were performed as described by Garibay-Orijel et al. (2013). To identify the host plant from the root tips, we amplified the *rbcL* and *trnL* regions using the *rbcL*-*a*F/*rbcL*-*a*R and trnC/trnD primer pairs (Kress and Erickson 2007). All of the PCR products were observed in 1 % agarose gels stained with GelRed (Biotium, Hayward, CA, USA). Amplicons of the appropriate size were cleaned with ExoSAP-IT (Affymetrix, Inc.). DNA sequences were generated in both directions using PCR primers and

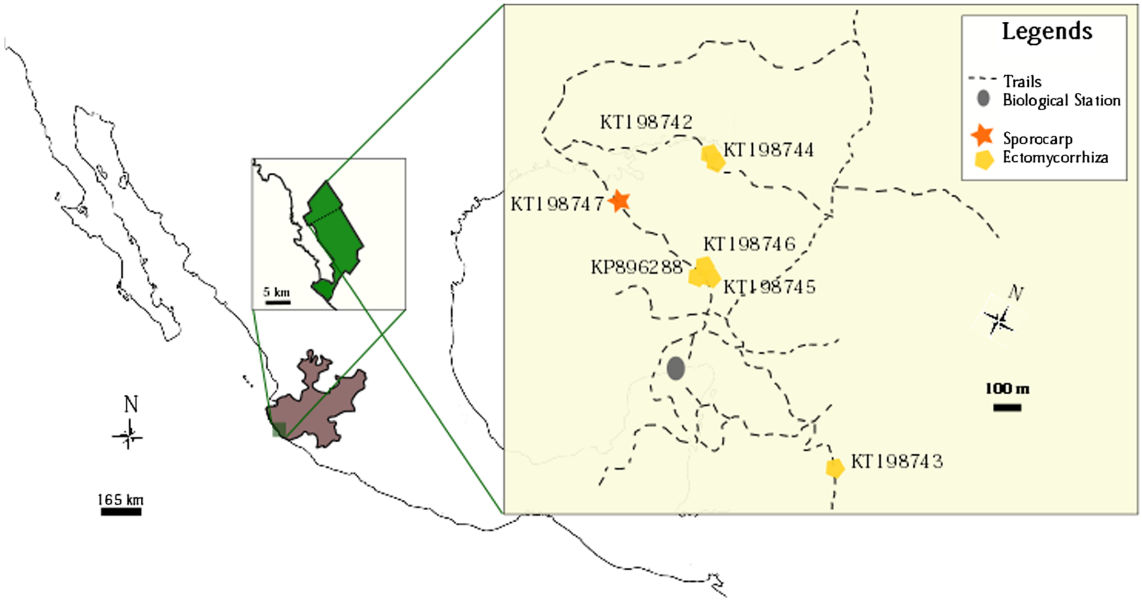

Fig. 1 Location of the Chamela-Cuixmala Biological Reserve, and distribution of the holotype fruit body and ectomycorrhizae of *Tomentella brunneoincrustata*. Samples are indicated by their GenBank accession numbers

BigDye Terminator v3.1 chemistry at the "Laboratorio de Secuenciación Genómica de la Biodiversidad y de la Salud" at the UNAM Biology Institute with an ABI PRISM 3100 genetic analyzer (Applied Biosystems, Foster City, CA, USA).

Bioinformatics The DNA sequences were edited and assembled using Geneious 6.1.4 software (Biomatters Ltd., Auckland, New Zealand). The plant hosts were identified by comparing the DNA sequences with those available in the BOLD Systems genetic barcode database. The identity of the fungal DNA sequences was assessed by phylogenetic analysis. First, we compared the sequences obtained in the present study against those in the GenBank and UNITE databases and downloaded all of the best matches (≥90 % similarity). We included all the tropical /tomentella-thelephora sequences from fruit body vouchers like those from the Seychelles (Suvi et al. 2010) and Benin (Yorou et al. 2011). We also selected environmental samples of /tomentella-thelephora from the Neotropics in GenBank and included *Tomentella* fruit body voucher sequences collected throughout Mexico in recent years by our laboratory (Table S1). The alignment was performed using MAFFT v7 (http://mafft.cbrc.jp/alignment/server/) and revised it manually with Mesquite v2.75. The molecular phylogenetic analyses included a Bayesian analysis that was performed using MrBayes v3.2.2 with 4 MCMC, 5 million generations, and three partitions (ITS1, 5.8S, ITS2). To select the best substitution model for each partition, we performed a reversible-jump Markov chain Monte Carlo computation (Pagel and Meade 2006) with *Thelephora terrestris* as the external group. We generated the consensus tree, adding posterior probabilities on the branches (≥0.75), and the nodes were depicted in decreasing order with FigTree v1.0.4.

Results

The ITS sequences of the six selected root tips and one sporocarp had an overall nucleotide sequence similarity of 98.3 %. The collection sites of these samples were widely distributed across the tropical dry forest of Chamela (Fig. 1). The Bayesian analysis grouped these sequences into a clade together with an ECM sequence from Dominica (JX548248), with high support (BPP = 1). The sequence from Dominica demonstrated an overall nucleotide sequence similarity of 96.8 % with the samples representing *T. brunneoincrustata*, and it contained 12 unique single-nucleotide polymorphisms (SNPs) (Table S2). This clade, together with two clades consisting of environmental samples of ECM from subtropical forests in Florida and tropical dry forests in Puerto Rico, made up the "Pisonieae-associated Neotropical *Tomentella* clade" (Fig. 2). Analysis of the *rbcL* and *trnL* sequences from the ECM revealed that five of the ectomycorrhizae were associated with a member of the Pisonieae tribe in the Nyctaginaceae and that one was associated with *Pisonia* sp. (Table 1). The sister clades from Puerto Rico and Florida were also associated with hosts in the Nyctaginaceae family (Fig. 2). Our samples belong to an undescribed clade with unique morphological and ecological characteristics, which is described here as the new species *Tomentella brunneoincrustata.*

The Bayesian analysis revealed that the *Tomentella* fruit body vouchers collected in temperate forests of Mexico belong to clades with species inhabiting temperate forests worldwide. KC152246 and KT353045 are related to *T. atramentaria* from the USA, Estonia, and Austria; KT353044 and KC152245 are a sister group of *T. pilosa* from Estonia and Sweden; KT353054 and UDB018512 formed a group with *T. muricata* from Estonia and Finland; KT353055 is related to *T. fuscocinerea* from Iran; KT353058 is a sister group of *T. stuposa* from Austria; KC152248 is related to *T. punicea* from China; and KT353052 is similar to *T. atroarenicolor* from Russia. We also found that KT353049, KT353048, and KT353047 are sister groups of *T. bryophila* from Scotland and Canada; however, this species is paraphyletic. The same case was found for KT353051, which is related to *T. lateritia* from Italy. Five fruit body vouchers had unique sequences (i.e. KC152247, KT353046, KT353056, KT353057, and KT353050) that formed independent and unknown clades of *Tomentella*.

Taxonomy

Tomentella brunneoincrustata M. Villegas & Contreras-Pacheco, sp. nov.

MycoBank: MB814303

Diagnosis Basidiome resupinate, crustose, thin, adherent to the substrate, dark brown, undifferentiated sterile margin, without rhizomorphs. Subicular hyphae dimitic, dark brown or purple brown; basidia subclavate, tetrasporic, clamped at base, rarely with transverse septa. Basidiospores subglobose to ellipsoid, dark brown, (6) 6.0–7.5 (8) × 5.5–6.5 μm; ornamentation echinulate, frequently bi- or trifurcate. Inhabiting soil and dead wood on tropical dry forests, forming ectomycorrhizae with different members of the Nyctaginaceae family. HOLOTYPE: Álvarez-Manjarrez 152b, (MEXU 27661).

Basidiome resupinate, thin, less than 1 mm thick, crustose, mostly continuous, indeterminate edges with patches around, strongly adherent to the substrate; hymenium dark brown (2.5/2–3/7.5 YR Munsell), smooth to the naked eye, densely tomentose and iridescent when seen under a dissection microscope, turns darker in 2.5 % KOH; subiculum concolorous

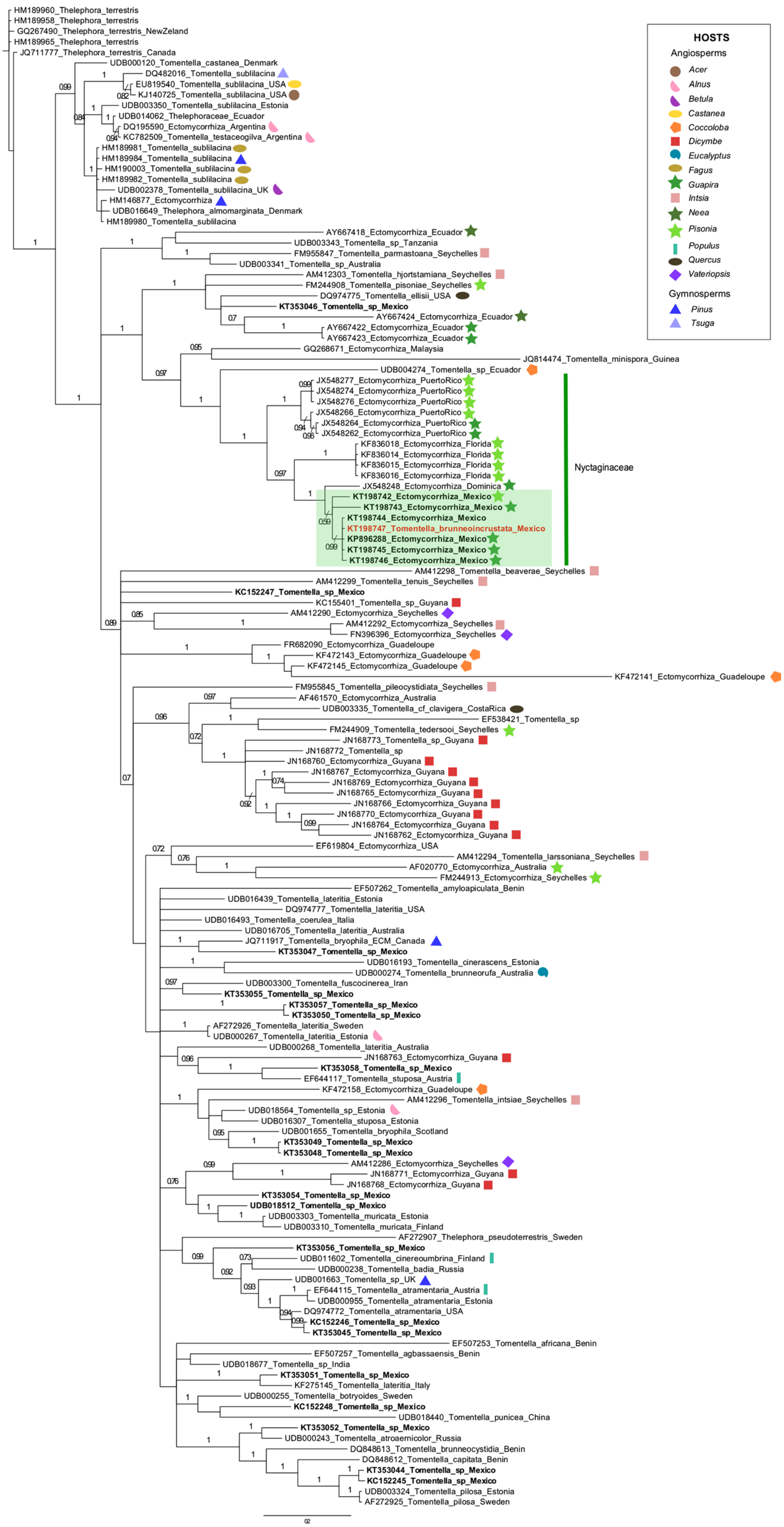

Fig. 2 Phylogenetic Bayesian analysis of vouchers and environmental samples of *Tomentella* and its host preferences. The sequences from *Tomentella brunneoincrustata*, including the ectomycorrhizae and the holotype, are shown in *bold* in a *green square*. The terminals indicate the regions where they were collected; sequences from environmental samples are labeled as "ectomycorrhiza" and sequences of *Tomentella* vouchers are labeled with the species names. The symbols indicate the host family: Aceraceae (*circle*), Betulaceae (*half-round*), Dipterocarpaceae (*diamond*), Fabaceae (*square*), Fagaceae (*oval*), Myrtaceae (*spiral*), Nyctaginaceae (*star*), Pinaceae (*triangle*), Polygonaceae (*pentagon*) and Salicaceae (*bold line*)

Table 1 BLAST identification of the ECM host *rbcL* and *trnL* regions

Sample type	Accession number GenBank	rbcL BLAST results		*trnL* BLAST results		Host
		% Id	Match	% Id	Match	
ECM	KT906429	100	*Pisonia aculeata* (KJ594427)	–	–	Pisonieae sp.
ECM	KT906430		*Neea psychotrioides* (JQ592987)	–	–	
ECM	KT906431		*Guapira standleyana* (GQ981748)	–	–	
ECM	KT906428			–	–	
ECM	KT906427					
ECM	KT906432			95	*Pisonia albida* (JX8444286)	*Pisonia* sp.

with the hymenium, undifferentiated sterile margin, rising slightly from the substrate; rhizomorphs absent (Fig. 3a).

Subicular hyphae consisting of two types: a) very common generative hyphae, dark brown in 2.5 % KOH, 3.2–5.1 (6.3) μm wide, thick-walled (up to 1 μm), clamped, branched mostly at right angles, with irregular swellings of up to 20 μm in some hyphae, anastomoses not observed, hyphae not congophilous, not cyanophilous and not amyloid (Fig. 3b); b) infrequent hyphae with simple septa, purple-brown, thin-walled, sometimes dichotomously branched, 1.8–3.3 μm wide, very ornamented on the surface with fine crystals insoluble in 2.5 % KOH, and not cyanophilous (Fig. 3c).

Subhymenial hyphae consisting of swollen cells with irregular forms, 4.2–11.1 μm wide, thick-walled (up to 1 μm), clamped, dark brown to light brown in 2.5 % KOH, and not congophilous or cyanophilous. Immature basidia dark brown in 2.5 % KOH, clavate, sphaeropedunculate or napiform, clamped and thick-walled; mature basidia 29.1–37.5 × 9.26–15.8 μm, subclavate, four sterigmata (5–7 μm), slightly thickened wall at the base and thin wall at the apex, light brown in 2.5 % KOH, clamped at the base, rarely exhibiting

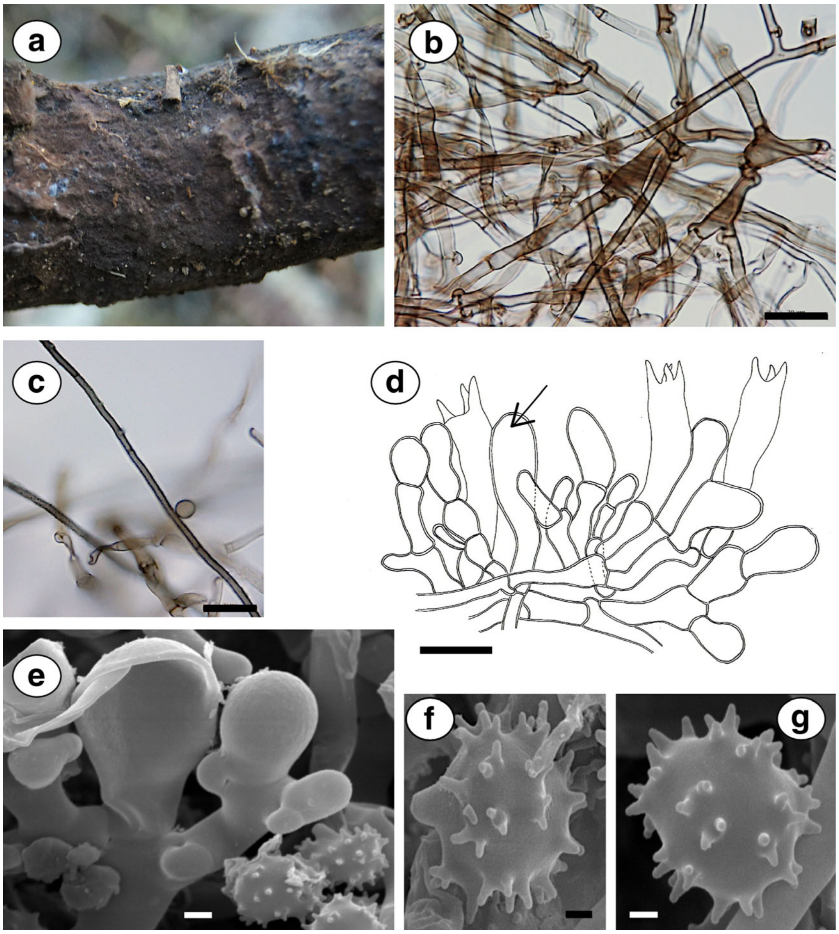

Fig. 3 *Tomentella brunneoincrustata* holotype (Alvarez-Manjarrez 152b). **a** Resupinate basidiome; **b** generative hyphae of subiculum with irregular swellings; **c** ornamented hyphae of subiculum; **d** sub-hymenium hyphae, immature basidia (*arrow*) and tetrasporic basidia; **e** SEM of young basidia with clamp at the base; f, g SEM of basidiospores in lateral and basal view showing obtuse hilar appendix and bi- or trifurcate ornamentation. Scale bars: **b**, **c** = 20 μm; **d** = 15 μm; **e** = 3 μm; **f**, **g** = 1 μm

transverse septa, and most septa collapsed (Fig. 3d, e). **Basidiospores** (6) 6.0–7.5 (8) × 5.5–6.5 μm (Q = 1.1–1.3 μm, Q = 1.1 μm, L = 6.8 μm, W = 6.1), in front view, subglobose to ellipsoid, some slightly lobed, dark brown in 2.5 % KOH, slightly thickened wall and echinulate, not congophilous, not cyanophilous, not amyloid. In SEM, spores showed an obtuse hilar appendix, 1–1.5 × 1.2–1.5 μm; echinulate ornamentation frequently bi- or trifurcate, 1–1.2 × 0.5–1 μm, with rounded or sub-rounded tips (Fig. 3f, g).

Remarks This species is characterized by a thin basidiome that is crustose and strongly attached to the substrate; subiculum concolorous with the hymenium, undifferentiated and sterile margin; two types of subiculum hyphae, of which the ornamented one does not present clamps; and small globose to ellipsoid spores (<8 μm). Among the tropical species described in the literature, this species is similar only to *Tomentella minispora* Yorou et al. (2012a) from Guinea, which also possess basidiomes, strongly attached to the substrate basidiomes, no rhizomorphs, clamps on both hyphae and basidia, ornamentation on the surface of some hyphae, and has a similar spore size. Despite this apparent similarity, *T. minispora* displays important differences, such as the presence of a differentiated sterile margin with clearer pigmentation, hyphae from the subiculum that are thin-walled or slightly thickened, hyphae ornamentation that is present only on the subhymenium, and spore ornaments that are never bi- or trifurcated.

Etymology From the Latin *brunneus* and *incrustata*, in reference to the brown color of the basidiome and extracellular incrustations on the hyphae of the subiculum.

Habit, habitat, and distribution This species develops in tropical dry forests in which it associates with hosts in the Pisonieae tribe within the Nyctaginaceae.

Specimens examined HOLOTYPE: Mexico, Jalisco, La Huerta municipality, Estación de Biología de Chamela, Tejón sidewalk, 19°30' N, 105°39' W, 26 Nov 2014, Álvarez-Manjarrez 152b, (MEXU 27661).

Anatomical description of the ectomycorrhizae

Tomentella brunneoincrustata + Pisonieae sp.

Ectomycorrhiza sinuous with monopodial ramifications and rounded tips. Completely black with emanating black and erect hyphae (Fig. 4a, b). **Mantle** thick and partially shiny, with 12–16 hyphal layers consisting of three different conformational structures. **External mantle** black, emanating hyphae septate with clamps, thick walls (>1 μm), and rounded terminations. **Internal mantle** has clearer hyphae in comparison with the remaining mantle, hyphae epidermoid or irregular (4–11 × 4–13 μm). **Hartig net** is prominent, peri-epidermal, enclosing the epidermal and the first cortical cell layer, infrequently lobulated (Fig. 4c, d).

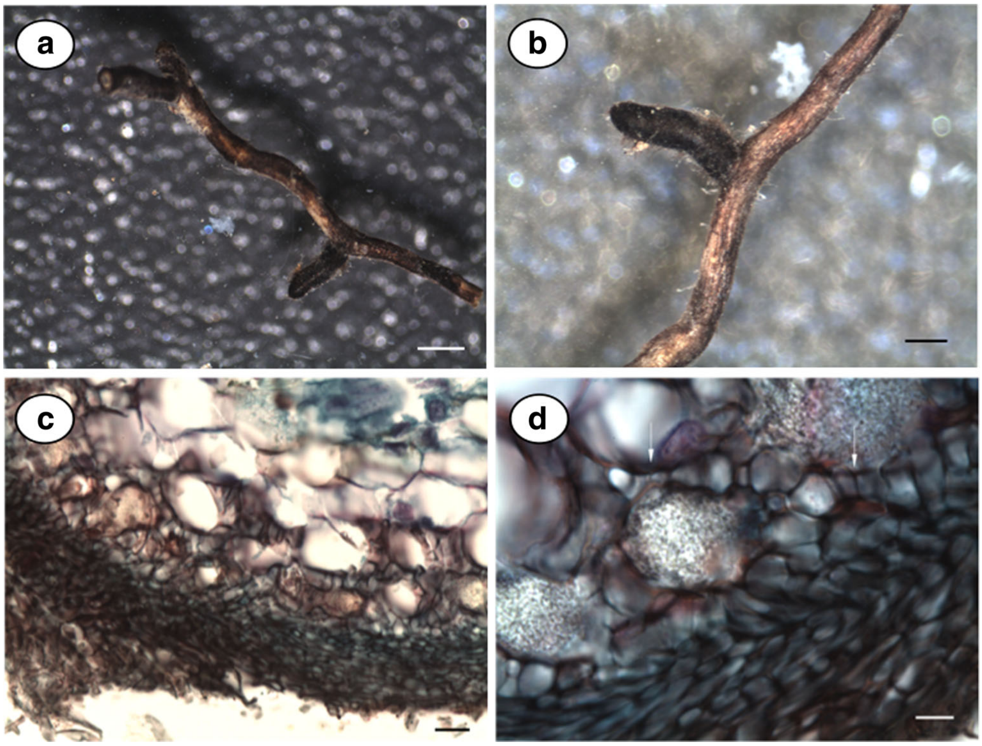

Fig. 4 **a-b** Ectomycorrhiza of *Tomentella brunneoincrustata* associated with Pisonieae sp. **c** Transversal section of an ectomycorrhizal tip showing the hyphal layer of the mantle and the peri-epidermal Hartig net. **d** Detail of the Hartig net, with *arrows* indicating the peri-epidermal hyphae. Scale bars: **a** = 0.5 mm; **b** = 0.25 mm; **c** = 75 μm; **d** = 4.5 μm

Tomentella brunneoincrustata + *Pisonia sp.*

Ectomycorrhiza sinuous with monopodial ramifications and rounded tips. Mantle black and extremely dense, tomentose-granulose surface and emanating hyphae dark in color. Hyphae more abundant and larger at the base of the ECM (Fig. 5a, b). **Mantle** with 10–17 hyphal layers (46–72 μm), resembling divergent lamellar trama. **External mantle** presents cylindrical, emanating straight hyphae (2–4 × 7–19 μm) with dark septa and a wide wall (<1 μm). **Internal mantle** has epidermoid lighter-coloured hyphae (4–8 × 3–7 μm). **Hartig net** hyaline, infrequently lobed, penetrating more than 1 cortical cell (Fig. 5c, d).

Considerations This species forms very similar morphotypes with different Nyctaginaceae hosts, consisting of a black, dense mantle with short exploration type (Agerer 2001) and with monopodial ramifications. The Hartig net is prominent, peri-epidermal, and infrequently lobulated.

Discussion

Tomentella brunneoincrustata produces dark brown fruit bodies that are somewhat similar to those of *T. agbassaensis* Yorou, *T. amyloapiculata* Yorou, *T. guineensis* Yorou, *T. guinkoi* Yorou, *T. minispora* Yorou, *T. afrostuposa* Yorou, and *T. intsiae* Suvi & Kõljalg. Another important characteristic of *Tomentella brunneoincrustata* is its adherence to the substrate and absence of rhizomorphs, both of which are observed in *T. amyloapiculata, T. guineensis, T. guinkoi, T. minispora,* and *T. intsiae*. This new species exhibits greater similarity to *T. minispora* and *T. afrostuposa* due to a common arachnoid subiculum, hymenia exhibiting the same color, and some sub-hymenial hyphae with incrustations. The size of the spores coincides with that of *T. minispora*. Nonetheless, *T. brunneoincrustata* presents unique characteristics: a diffuse concolorous margin, non-cyanescent subiculum hyphae, hyphal ornamentation that is present only on the subiculum, and spore ornaments that are bifurcate or trifurcated.

The fruit body of the holotype was found on the underside of a piece of wood without evident rotting. *Odontia,* the sister genus of *Tomentella*, has been reported to be saprotrophic (Tedersoo et al. 2014). However, *T. brunneoincrustata* forms ECM and belongs to an ectomycorrhizal clade that is associated with the Pisonieae tribe from the Nyctaginaceae. This is the first study to describe a *Tomentella* species from the Neotropics, including its ectomycorrhizae. The ECM of this species displayed a dense, dark brown mantle; the Hartig net was found to be peri-epidermal and very prominent in both morphotypes. This species shares only the dark mantle with the *Tomentella* EMC morphotypes described by Jakucs and Erõs-Honti (2008) and Jakucs et al. (2015). The ECM of this species exhibits greater similarity to the one described for the *Guapira* ECM from Ecuador (Haug et al. 2005), which shares the prominent Hartig net. However, *T. brunneoincrustata* develops a mantle wrapping the root tips completely, with the Hartig net penetrating two cell layers.

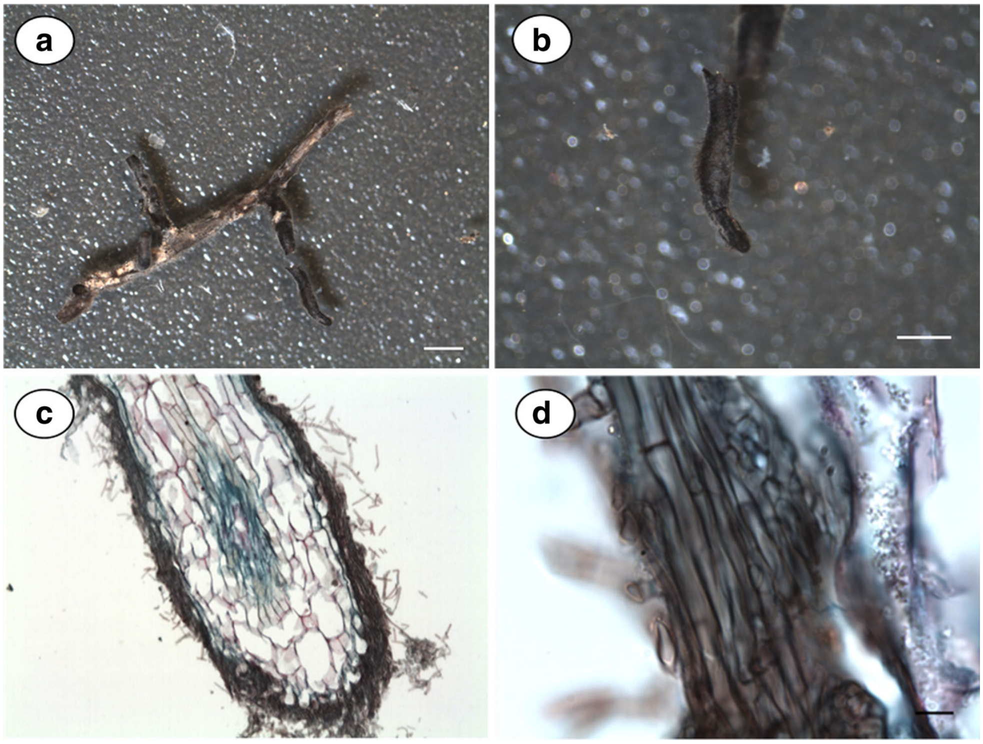

Fig. 5 **a**-**b** Ectomycorrhiza of *Tomentella brunneoincrustata* associated with *Pisonia* sp. **c** Transversal section of the ectomycorrhizal tip (10×). **d** Detail of the dark mantle. Scale bars: **a** = 1.0 mm; **b** = 0.5 mm; **d** - 4.5 μm

In phylogenetic analysis, the sequence of the ECM from Dominica exhibited the closest similarity to those from *T. brunneoincrustata* (96.3 % similarity). However, according to the 97 % similarity consensus to form MOTUs of ECM fungi (Nilsson et al. 2008; Peay et al. 2008; Setaro et al. 2012) and the UNITE species hypothesis of 98 % (Kõljalg et al. 2013), this sequence is not included with *T. brunneoincrustata*.

Although genetic markers that are recognized as genetic barcodes for plants were used for host identification, we were able to identify only one host to genus level, *Pisonia* sp., according to the list of plants from Chamela (Lott 1993). The reserve contains 13 species from 8 genera of Nyctaginaceae; *Guapira petenensis* is the unique species in this genus, while *Pisonia* has two species, *P. aculeata* and *P. macranthocarpa*.

The association of /tomentella-thelephora with Pisonieae has been reported in several regions throughout the world: Dominica, Ecuador, Florida, Hawaii, Puerto Rico, Rota, the Seychelles, and Vieques (Haug et al. 2005; Hayward and Horton 2012, 2014; Suvi et al. 2010, Tedersoo et al. 2010b). Bayesian analysis showed that several paraphyletic clades within the lineage /tomentella-thelephora are associated with Pisonieae across the tropical regions of the world. However, the ECM sequences from Puerto Rico, Florida, Dominica, and Mexico constitute the “Pisonieae-associated Neotropical *Tomentella* clade”, which is monophyletic and inhabits tropical dry and subtropical forests of the Neotropics, especially the Mesoamerican and Caribbean regions. The specificity of this fungal clade to the Pisonieae supports the hypothesis of partner choice phylogenetic trait conservation proposed by Hayward and Horton (2014).

The Pisonieae tribe includes three ectomycorrhizal genera: *Guapira, Neea,* and *Pisonia*. *Neea* and *Guapira* are paraphyletic groups (Hayward and Horton 2014), both of which are exclusive to tropical forests in Mexico, Central America, and South America (Douglas and Manos 2007). There are three *Guapira* species, eight *Neea* species, and five *Pisonia* species in Mexico. These species are distributed in 25 of the 32 Mexican states, among which Chiapas exhibits the greatest diversity, with 13 spp., followed by the Yucatan Peninsula with 11 spp. Given that *T. brunneoincrustata* is associated with two of these genera, there is a high probability that this species, or other undescribed species within the Pisonieae-associated Neotropical clade, has a wider distribution within the Neotropics. More systematic sampling of the entire area is needed to understand the biology, ecology, and diversity of *Tomentella* in the Neotropics.

Given the distribution and ecosystem preferences of the Pisonieae-associated Neotropical *Tomentella* clade, it is likely that this clade is associated with water stress conditions, such as in those present in the Chamela tropical dry forest. The samples from Puerto Rico and Dominica were also obtained from tropical dry forests (Hayward and Horton 2014). In Puerto Rico, the mean temperature is 29.7 °C, with a maximum of 32.4 °C, a minimum of 14.6 °C, and mean annual precipitation of 1687 mm. The distribution of water resources is critical in the Caribbean islands, and similar patterns are observed in different islands (Daly et al. 2003), such as Dominica. Even the samples from Florida inhabited a subtropical region with an average temperature of 23.8 °C and average rainfall of approximately 1524 mm per year, 75 % of which occurred from June through October, coinciding with hurricane season (Multer and Hoffmeister 1968). Thus, all of the members of this clade seem to develop in (sub)tropical areas with high temperatures and heterogeneous rainfall regimes that are unevenly distributed throughout the year.

Six species of *Tomentella* have been reported in Mexico; however, the Bayesian analysis revealed a large diversity of *Tomentella* species, some of which are related to known taxa, and many others which are likely new species. The *Tomentella* fruit body vouchers from temperate forests in Mexico that were included in the analysis showed greater genetic similarity with species from temperate climates than those from tropical climates. These results are consistent with the biology of the species and its host associations. Hayward and Horton (2014) noted that when *Neea buxifolia* and *Pisonia aculeata* were planted in New York soil, in which local thelephoroids were available, the plants failed to form ECM with the local species. The Nearctic and Neotropical biotas coincide in Mexico (Estrada-Contreras et al. 2015), and even if the vegetation types are similar (e.g., the transitions of pine-oak forest, montane cloud forest, tropical dry forest, and sand dunes), temperate and tropical tree species do not intermix, enabling a high diversity of many biological groups.

This is the first study to analyze the diversity of *Tomentella* in Mexico. The phylogenetic analysis presented here will help to guide future investigations designed to identify and describe the *Tomentella* species in this region. However, given the vast diversity and complexity of the genus in this country, a complete knowledge of its diversity and ecology is a long-term task that would require the participation of several research groups.

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