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ORIGINAL ARTICLE

Lepidostroma vilgalysii, a new basidiolichen from the New World

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Abstract The lichenized basidiomycete *Lepidostroma vilgalysii* from Mexico is described based on morphological analyses. The species is only the second representative of the family Lepidostromataceae documented from the New World, and is one of the few described lichens with an inverted morphology, with the algae in a layer at the base of the thallus. Molecular sequence data from the nuclear ribosomal LSU locus are used to confirm the placement of the holotype in *Lepidostroma* and to evaluate the molecular distinctiveness of the species from all other described species in the family and genus.

Keywords Lepidostromataceae · Basidiomycota · Lichen-forming fungi · Mexico · Trans-Mexican Volcanic Belt · Phylogenetic constraint

Introduction

While the vast majority of lichenized fungi belong to the phylum *Ascomycota*, there are several small clades with lichenized members that belong to *Basidiomycota* (Oberwinkler 1970). The thalli formed by these types of fungi are often collectively referred to as 'basidiolichens'. In contrast to the much more common 'ascolichens', the basidiolichens generally have fruiting bodies that are ephemeral like other mushrooms and club fungi, making the collection of fertile material a somewhat rare occurrence (Honegger 1996). As a result, basidiolichen species are often overlooked or may be impossible to identify due to a lack of sexual characters.

The basidiolichen genus *Lepidostroma* was established by Mägdefrau & Winkler (1967) to accommodate the New World species *Lepidostroma terricolens*. Subsequently, the type species has been reduced to synonymy with *L. calocerum* (G.W. Martin) Oberw. (Oberwinkler 1984). More recently, two additional species from Africa were described (Fischer et al. 2007) and transferred to the genus based on molecular data (Ertz et al. 2008). These new data also demonstrated that the unique genus warranted the creation of a new family, *Lepidostromataceae*, which cannot currently be placed definitively in any known fungal order (Ertz et al. 2008).

Within the established framework of these three well-characterized *Lepidostroma* species, we examine the phylogenetic and taxonomic position of a clavarioid fungus recently collected by Dr. Rytas Vilgalys from the Trans-Mexican Volcanic Belt that was sequenced and found to have molecular affinities to the genus *Lepidostroma*. We present the subsequent morphological and molecular analyses that revealed it to be a representative of a previously undescribed species.

Materials and methods

Morphological analyses The specimen RV-MX16 and collections representing all described members of the genus

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were studied dry using a Bausch & Lomb StereoZoom 7 dissecting microscope and wet using an Olympus BX51 compound microscope. Images were captured using an Olympus DP20 digital camera with the MicroSuite Special Edition 5.0 software package (Olympus, Tokyo, Japan), and illustrations were prepared using Photoshop CS3 (Adobe, San Jose, California). The specimen RV-MX16 was divided, with one portion being deposited at The New York Botanical Garden Herbarium (NY) and the other being deposited in the Duke University Herbarium (DUKE).

Molecular protocols Dried sporocarp tissue of RV-MX16 was homogenized with a sterile micropestle and DNA was extracted with the DNeasy Plant Mini Kit (Qiagen, Valencia, CA USA). The nuclear ribosomal large subunit (LSU or 28S) was PCR-amplified with the primer combination LROR/LR5F using published protocols (Vilgalys and Hester 1990, Tedersoo et al. 2008). PCR products were viewed on 1.5% agarose gels stained with SYBR Green I (Molecular Probes, Eugene, Oregon). Amplicons were cleaned with EXO (Exonuclease I) and SAP (shrimp alkaline phosphatase) enzymes (Glenn and Schable 2005) and sequenced with the Big Dye 3.1 kit (Applied Biosystems, Foster City, California) using the same primers used for amplification. Sequencing reactions were cleaned and then processed on an ABI 3730xl genetic analyzer (Applied Biosystems, Foster City, California) at the Duke University Genome Sequencing & Analysis Core Facility. Newly generated sequence reads were edited using Sequencher 4.9 (Gene Codes Corp., Ann Arbor, MI). The final corrected sequence was subjected to a BLASTn search as outlined by Hodkinson et al. (2010), using NCBI's non-redundant nucleotide collection from May 2011 (Altschul et al. 1997), and subsequently deposited in GenBank under accession number JN698908.

Phylogenetic analyses The full LSU data set assembled by Ertz et al. (2008) was used as a reference for phylogenetic inference. Sequences from Ertz et al. (2008) were downloaded from GenBank in FASTA format and edited using a customized Perl script, 'sequence_renamer.pl', available in the data package associated with this manuscript, deposited in the Dryad data repository (http://datadryad.org/; data package URL: http://dx.doi.org/10.5061/dryad.j1g5dh23; data package DOI: 10.5061/dryad.j1g5dh23; Hodkinson et al. 2011). All sequences were aligned using default settings in MAFFT 6.853 (Katoh et al. 2002; http://mafft.cbrc.jp/alignment/server/) and adjusted by hand with Mesquite 2.74 (Maddison & Maddison 2010). Phylogenetic analyses were performed on the portion of the LSU region that overlapped in all of the *Lepidostroma* sequences, both those generated for this study and those stored in GenBank. Ambiguously-aligned regions were excluded, and RAxML-HPC-SSE3 7.2.8a (Stamatakis, 2006) was run using a backbone constraint tree. The constraint tree consisted of the terminals in the tree presented by Ertz et al. (2008) (with the exception of *Athelia arachnoidea* MYA-3672, which lacked LSU sequence data) and contained only nodes supported by maximum likelihood (ML) bootstrap proportions (BP) ≥70% in Ertz et al. (2008). One thousand topology searches and an equal number of bootstrap pseudo-replicates were performed under the GTRGAMMA model, and RAxML-HPC 7.0.4 was used to map BP values to the best topology. The tree was visualized with FigTree 1.2.3 (http://tree.bio.ed.ac.uk/software/figtree/), and Illustrator CS4 (Adobe, San Jose, California) was used to make the final phylogeny figure. The analyzed alignment file was formatted for and deposited in TreeBASE (http://www.treebase.org/; study accession URL: http://purl.org/phylo/treebase/phylows/study/TB2:S12029; submission 12029) and analysis files were made available through the Dryad data repository (http://datadryad.org/; data package URL: http://dx.doi.org/10.5061/dryad.j1g5dh23; data package DOI: 10.5061/dryad.j1g5dh23; Hodkinson et al. 2011).

Pair-wise sequence analyses A pair-wise distance matrix of *Lepidostroma* LSU sequences was created to examine variation between both members of the same species and members of different species. The portion of the LSU gene that was sequenced for all samples was isolated for analysis from the full nucleotide alignment using Mesquite 2.74 (Maddison & Maddison 2010). Sites with polymorphisms due to a single sequence differing from all others were treated as suspicious, since sequencing errors can easily produce such polymorphisms; therefore, sites that were unambiguously-aligned and had only one sequence that differed from the others were excluded from pair-wise distance calculations. Unambiguously-aligned sites with ambiguous base calls were additionally excluded. Pair-wise distances between unaligned sequences were calculated by executing the 'pairwise.seqs' function with default settings in Mothur 1.19.2 (Schloss et al. 2009).

Results

Morphological analyses revealed yellow to orange-brown basidiocarps with distinctively cream-colored tips; these tips are especially apparent when dry (Fig. 1a-c). The squamules have a white, raised margin (Fig. 1a-b) that becomes less distinct as squamules mature or become wet (Fig. 1d). The squamules' upper surfaces are maculate (Fig. 1d) due to columns of photobiont cells projecting upward from the main algal layer at the base (Fig. 1e). Elongate-ovoid spores on bi-sterigmate basidia were observed (Fig. 1f) on the fruiting bodies, and the upper cortex of the squamules was

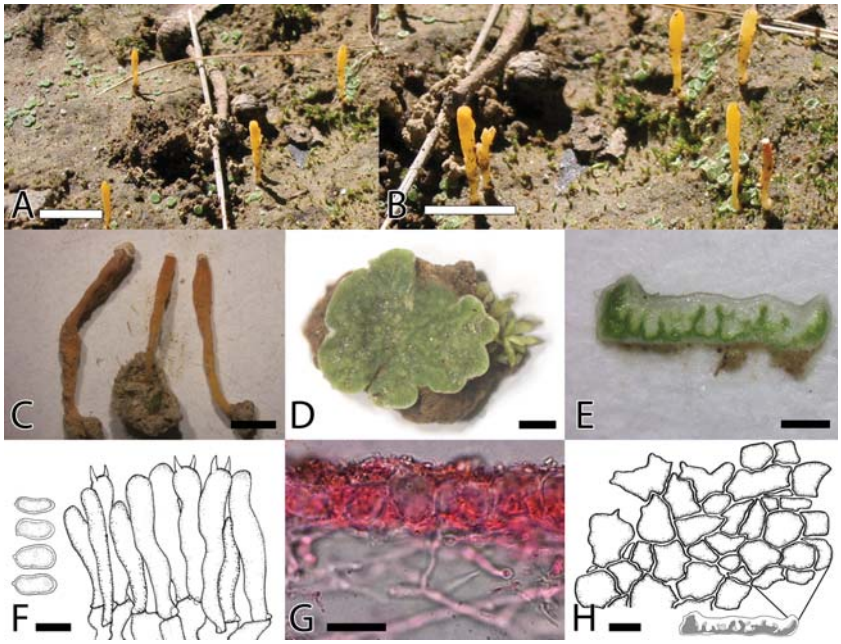

Fig. 1 Habit and morphology of *Lepidostroma vilgalysii*. Images and drawings show the habit (A-B; scale bars=1 cm), basidiocarps with light-colored apices (C; scale bar=2 mm), a wet expanded squamule as seen from above (D; scale bar=0.5 mm), a squamule cross-section with the algal layer projecting upwards in pyramidal or irregular columns (E; scale bar=0.5 mm), bi-sterigmate basidia and spores (F; scale bar= 10 μm), a section through the upper cortex of a squamule (stained with phloxene) showing a portion of the cortex with a single cellular layer (G; scale bar= 10 μm), and a view downward on the upper cortex of a squamule with polygonal cells (H; scale bar=10 μm for the drawing of the upper surface only)

seen to be comprised of polygonal (in both side view and from above) cells that were sometimes in a single layer and sometimes in multiple layers (Fig. 1g-h). The overall squamule morphology and other features not mentioned here (but described below in the taxonomic section) are similar to those described for the species *L. rugaramae*.

The phylogenetic inference places the new species within a clade comprised of all defined species in the genus *Lepidostroma* (Fig. 2). Finer-scale relationships between the species within the genus could not be resolved with confidence using the present molecular data set. A pairwise analysis of all LSU sequences generated for members of the genus shows that distances between sequences within species range from 0 to 0.013, while the distances between sequences representing different species fall within the range of 0.019 to 0.096 (Table 1).

The new species

LEPIDOSTROMA VILGALYSII HODKINSON, **SP. NOV.** (Fig. 1)

Mycobank Number: 563511

Diagnosis A *Lepidostroma rugaramae* basidiocarpis pallidioribus, cellulis polygoniis corticis superi, basidiosporis longioribus, et in Americas distributione geographica differt. Holotypus (hic designatus): RV-MX16.

Holotype Mexico, Tlaxcala, San José Teacalco, Camino Perimetral near the Albergue del IMSS, 19°17'26"N, 98° 2'65"W, 3,015 m asl., on clay bank soil, in forested area with *Pinus montezumae* and *Alnus acuminata*, R. Vilgalys (RV-MX16), 21. 9. 2007. Holotype (NY) [Isotype (DUKE)].

Description THALLUS distinct, green to dark green, composed of dispersed (never confluent), rounded patches, up to 0.2–0.5 mm thick and 1.5–2.5(–3.0) mm in diameter, expanding when wet, becoming hardened when dry. Squamules concave, with a conspicuous, whitish, raised and somewhat swollen margin; when mature having a less conspicuous margin and almost flat. Rhizohyphae ('rhizinomorphs') abundant and extending from the lower surface, going 1–4 mm under the squamules; hyphae forming rhizohyphae thin-walled, 3–5 μm thick, with clamps. Upper surface pale to deep green with lighter-colored maculae. Upper cortex pseudoparenchymatous, composed of 1—3 layers of cells that are polygonal (not jigsaw-like) in both side and surface view and are variable in shape and size, cells 5—15 μm across (cells smaller when multiple layers are present); lower cortex composed of multiple cell layers with rhizohyphae extending below. Medulla loose, 0.15–0.40 mm thick, with anastomosed and sparsely branched hyphae, 1.0–3.5 μm thick; algal cell layer dense and compact in the lower part of the medulla and projecting upwards in pyramidal or irregular columns, up to half or three-quarters of the medulla height. Photobiont: chlorococcoid colonies with mostly ellipsoid green cells, 8—13 x 5—8 μm, with a (sub)central pyrenoid. BASIDIOCARPS club-shaped, simple, 0.5–1.2 cm long, 0.3–0.6(–1.0) mm thick and brittle when dry, pale yellow to rusty orange-brown, usually with bottom half lighter, top half darker, and the apex a pale cream color when mature, surface with a few distinct and irregular longitudinal furrows when dry; hymenium *c*. 50 μm thick.

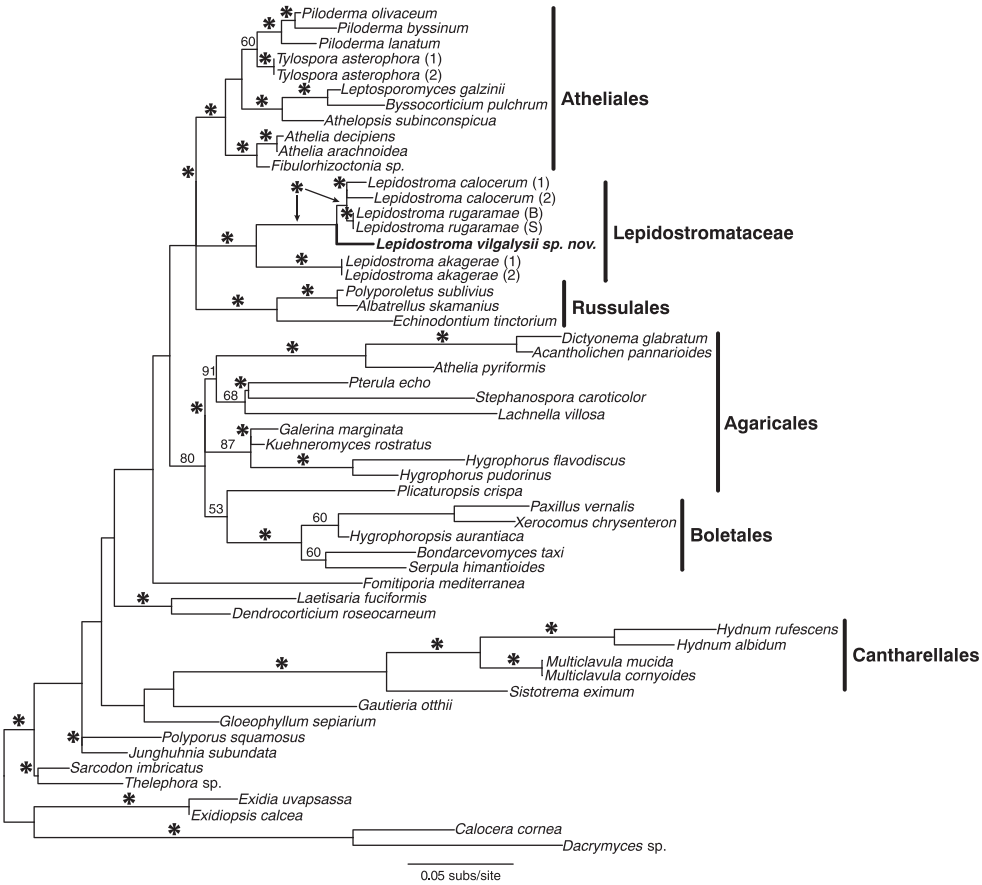

Fig. 2 RAxML phylogeny based on partial nuclear ribosomal LSU sequence data showing a phylogenetic placement of *Lepidostroma vilgalysii*. Asterisks indicate nodes that were phylogenetically constrained; the constraint tree contained every terminal in the final tree except for the new species and had only nodes with >70% ML-BP in Ertz et al.'s (2008) LSU + SSU tree. ML-BP >50% are given for the nodes that were not constrained. GenBank Accession numbers for the reference sequences are listed by Ertz et al. (2008), and correlated GenInfo identifier numbers are specified in the supplementary alignment file (Dryad data package URL: http://dx.doi.org/10.5061/dryad.j1g5dh23; doi:10.5061/dryad.j1g5dh23; Hodkinson et al. 2011)

Central hyphae orange, present in the top half of the basidiocarp (where the basidiocarp widens), densely agglutinated and rounded to distinctly polygonal in cross-section, thin-walled, simple or rarely branched, with clamps present throughout the basidiocarp. Sterile elements apparently present in the hymenium. Basidia subclavate or clavate, 30–45 x 7–10 μm, basally clamped, with two sterigmata. Basidiospores elongate-ovoid, thin-walled and hyaline, with an apiculus that is typically small and eccentric, with guttules, 11—14 μm x 4—6.5 μm (measured in KOH).

Etymology The species is named after Dr. Rytas Vilgalys, who collected the type and has been a major force in the field of mycology over the past several decades.

Taxonomic notes The thallus of *Lepidostroma vilgalysii* most closely resembles *Lepidostroma rugaramae* (since both species have maculae and white-rimmed squamules), but the cells of the upper cortex are polygonal (not jigsaw-like) when viewed from above and are sometimes in multiple layers (as opposed to the strictly single-layered cortical

Table 1 Pair-wise distances between *Lepidostroma* nuclear ribosomal LSU sequences. Italicized values represent distances between sequences from members of the same species (range=0—0.013), while values in bold represent distances between *L. vilgalysii* and members of other species (range=0.019—0.090). GenBank Accession numbers are given as sequence identifiers; correlated GenInfo Identifiers for these sequences are specified in the supplementary alignment file (Dryad data package URL: http://dx.doi.org/10.5061/dryad.j1g5dh23; doi:10.5061/dryad.j1g5dh23; Hodkinson et al. 2011)

	FJ171733	FJ171734	FJ171737	FJ171738	FJ171735	FJ171736
L. akagerae FJ171733	-					
L. akagerae FJ171734	*0*	-				
L. calocerum FJ171737	0.084	0.084	-			
L. calocerum FJ171738	0.088	0.088	*0.013*	-		
L. rugaramae FJ171735	0.096	0.096	0.021	0.019	-	
L. rugaramae FJ171736	0.096	0.096	0.021	0.019	*0*	-
***L. vilgalysii* JN698908**	**0.090**	**0.090**	**0.021**	**0.019**	**0.019**	**0.019**

morphology of *L. rugaramae*). With regard to the basidiocarps, those of the new species do not show the reddish tinge found in those of *L. rugaramae*. Furthermore, *L. rugaramae* is known only from central Africa, whereas *L. vilgalysii* has only been found in Central America. The only other species in the genus known from the New World is *L. calocerum*. The thallus of *L. calocerum* differs from that of the new species by having reniform to deeply lobate, rarely rounded, squamules without a swollen, whitish margin or maculae. The only other species described in the genus is *L. akagerae*; while *L. akagerae* has discrete, turgescent, and slightly convex squamules that are contiguous or irregularly lobulate (*Botrydina*-type), all other members of the genus possess *Coriscium*-type thalli comprised of dispersed squamules that are typically either rounded (as in *L. rugaramae* and *L. vilgalysii*) or reniform to deeply lobate (as in *L. calocerum*) (Fischer et al. 2007). Additional features that distinguish *L. vilgalysii* from other members of the genus include the distinct, broad pale cream-colored apex that is most evident when dry; the basidiocarps are also often darker along the top half (with the exception of the cream-colored tip) and lighter as they taper toward the base. Other noticeably different features include the more elongate shape of the spores and the bisterigmate basidia. In addition to morphological evidence, the degree of molecular divergence seen in the LSU region between *L. vilgalysii* and all others in the genus indicates that this species is distinct from those previously described in the group (Table 1).

Distribution and habitat The species was first collected in 2007, on a clay embankment in *Pinus*-dominated forest at 3,015 meters above sea level near San José Teacalco in estado Tlaxcala, Mexico. Additional specimens representing the species could not be located.

Comparative material examined ***Lepidostroma akagerae* (Eb. Fisch., Ertz, Killmann & Sérus.) Ertz, Eb. Fisch., Killmann, Sérus. & Lawrey** – Rwanda, prov. Kibungo, Akagera National Park, foot of Mt. Mutumba, 01°38’51.6”S, 30°39’53.7”E, 1450 m asl., on open lateritic soil in burnt savanna, open savannas and wooded gallery thickets along a small intermittent river, D. Ertz (8556) with E. Fischer, D. Killmann, & E. Sérusiaux, 11. 4. 2005. Holotype (BR). – Rwanda, prov. Kibungo, Akagera National Park, foot of Mt. Mutumba, 01°38’51.6”S, 30° 39’53.7”E, 1450 m asl., on open lateritic soil in burnt savanna, open savannas and wooded gallery thickets along a small intermittent river, E. Sérusiaux with D. Ertz, E. Fischer, & D. Killmann, 11. 4. 2005. Isotype (LG). – Rwanda, prov. Butare, Butare, IRST park, 02° 37’0.20”S, 29°44’0.45”E, c. 1690 m asl., on earth embankment, with isolated trees on regularly cut meadows and plantations, E. Sérusiaux with D. Ertz, E. Fischer, & D. Killmann, 27. 3. 2005 (LG). ***Lepidostroma calocerum* (G.W. Martin) Oberw.** – Mexico, Puebla, Mpo. Teziutlan, 12 km W of Teziutlan on the road to Coaxisco, c. 2030 m asl., on ground, veg. bosque de pino alterado, J. Grimes (2731) with P. Tenorio & M. Martinez, 12. 4. 1985 (NY). ***Lepidostroma rugaramae* (Eb. Fisch., Ertz, Killmann & Sérus.) Ertz, Eb. Fisch., Killmann, Sérus. & Lawrey** – Rwanda, prov. Kibungo, 02°08’05.0”S, 30° 40’51.3”E, 1600–1690 m asl., on soil, quartzitic outcrops at Rugarama with sparse vegetation, E. Fischer & D. Killmann, 10. 4. 2005. Holotype (LG). – Rwanda, prov. Kibungo, Akagera National Park, Sports Fishing Camp at Lac Ihema, 01°52’25.1”S, 30°44’36.8”E, 1290 m, on lateritic crusts, *D. Ertz, E. Fischer, D. Killmann & E. Sérusiaux*, 11. 4. 2005 (LG) – Rwanda, prov. Kibungo, Nyarubuye, 02°08’54.0”S, 30°44’44.1”E, 1800 m, on soil, quartzitic outcrops with scattered trees and vegetation, *D. Ertz* (8544) [with *E. Fischer, D. Killmann, & E. Sérusiaux*], 10. 4. 2005 (BR).

Discussion

Both the placement of the new specimen within *Lepidostroma* and the distinction of it from members of all described species in the genus can be established based on morphological and molecular grounds. An analytical approach integrating these two types of data revealed a clear taxonomic solution for the material under investigation. We therefore describe the new species *Lepidostroma vilgalysii* to accommodate this specimen and encourage collectors to seek out additional material so that this entity can be evaluated for the purpose of conservation.

Morphological study of the type indicates that the thallus most closely resembles the central African species *Lepidostroma rugaramae*, as both species have white-rimmed squamules with conspicuous maculae (Fig. 1d) resulting from pyramidal photobiont columns (Fig. 1e). However, the basidiocarps are yellow to orange-brown, without the reddish tinge seen in *L. rugaramae*, and the apex is distinctively cream-colored, especially when dry (Fig. 1a-c). Additionally, the spores are more elongate, making them larger overall (Fig. 1f), and the cells of the upper cortex of the thallus are polygonal in surface view and often multi-layered (neither jigsaw-like in surface view nor consistently in a single layer as in *L. rugaramae*; Fig. 1g-h).

The new species is only the second New World species in the genus, along with *Lepidostroma calocerum*. The thallus of *L. calocerum* differs from that of the new species by having squamules that are reniform to deeply lobate, rarely

rounded, without any paler spots or maculae, and without a swollen, whitish margin. The full geographic range of *L. vilgalysii* is likely to overlap with *L. calocerum*, given that both species are known from the same portion of the Trans-Mexican Volcanic Belt.

The only other described species in the genus, *Lepidostroma akagerae*, has squamules which are discrete, turgescent, slightly convex, and contiguous or irregularly lobulate. These features of the squamules distinguish it from all other members of the family, including *L. vilgalysii*. The thallus of *L. akagerae* is known as '*Botrydina*-type', while all other members of the genus possess '*Coriscium*-type' thalli, which are comprised of dispersed squamules that are typically either reniform to deeply lobate (as in *L. calocerum*) or rounded (as in *L. rugaramae* and *L. vilgalysii*) (Fischer et al. 2007).

The molecular phylogeny shows the *Lepidostroma vilgalysii* specimen nested within the genus *Lepidostroma*, most closely related to *L. calocerum* and *L. rugaramae* (Fig. 2). Placement in a clade with these two species is congruent with morphological analyses; however, robust resolution of relationships between these three species will require additional sequence data. Based on pair-wise analyses of LSU sequences, the genetic distances between the *L. vilgalysii* sequence and sequences from other *Lepidostroma* species suggest that it is not conspecific with any of the described members of the genus (Table 1).

The species described here is interesting because it represents one of the rare cases of an inverted thallus morphology (with the algae growing primarily in a layer along the base of the thallus), a feature that can also be found in *Lepidostroma calocerum* and *L. rugaramae*. Lichens with these types of thalli are often referred to as 'window lichens' and occur rarely in disparate lineages (e.g., *Buellia*, *Lepidostroma*, *Peltula*), apparently as an adaptation to dry conditions (although this explanation may not be appropriate for *L. calocerum*) (Büdel & Schultz 2003; Ertz et al. 2008; Vogel 1955).

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