

Standard Paper

Diploicia edulis (Caliciaceae) and *Physcia ornamentalis* (Physciaceae), two new species associated with invertebrates from the tropical dry forest of Mexico

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Abstract

Two new species in the genera *Diploicia* and *Physcia* are described from the tropical dry forest of Mexico. Both species are supported by morphological, chemical and molecular evidence. *Diploicia edulis*, a species heavily consumed by invertebrates, is characterized by lecanorine apothecia, a dull brown epihymenium not diffused by a green pigment (K–), a subhymenium conspicuously interspersed with oil droplets, and the diploicin chemosyndrome. We provide the first molecular evidence to support the inclusion of species with lecanorine apothecia in the genus *Diploicia*. *Physcia ornamentalis*, previously reported under the name *Physcia undulata* s. lat. as one of the main construction materials for the bags of a moth caterpillar species (*Psychidae*), is characterized by a frosted-pruinose thallus, soralia originating in the lobe sinuses, and by lacking soralia in the thalline margin of the apothecia.

Keywords: Chamela-Cuixmala Biosphere Reserve; lichen systematics; new species; phylogeny; *Psychidae*

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Introduction

Interactions between lichens and animals are widespread. In tropical ecosystems, whether those interactions are related to food, shelter, or camouflage, they typically occur with invertebrates (Gerson & Seaward 1977). In the case of neotropical dry forests, lichen communities are dominated by crustose forms in terms of abundance and species richness (Miranda-González & McCune 2020), with several new species described in recent years (Herrera-Campos *et al.* 2019; Guzmán-Guillermo *et al.* 2021; Miranda-González *et al.* 2022a; Soto-Medina 2022). However, the use of lichens by invertebrates, beyond their use as food, typically favours the tridimensionality of foliose and fruticose forms (Miranda-González *et al.* 2023).

Although less abundant than crustose forms, macrolichens are also diverse in tropical forests (Aptroot & Cáceres 2014), with new species being described continuously (Miranda-González *et al.* 2022b). Given the widespread use of European names for American taxa and the availability of molecular techniques, many new species of tropical macrolichens are likely to be

reported in the coming years (Esslinger *et al.* 2020). Here, we describe two new species of (sub)foliose lichens associated with invertebrates from the tropical dry forest of Mexico. *Diploicia edulis* sp. nov. was found heavily covered by silk and faecal pellets, since invertebrates use it for shelter and food. *Physcia ornamentalis* sp. nov., referred to as *Physcia undulata* s. lat. in Miranda-González *et al.* (2023), is one of the primary materials *Psychidae* caterpillars use in their bag construction.

The genus *Diploicia* A. Massal. (*Caliciaceae*), with only nine species accepted so far (including the new species described here), is characterized by a placodioid thallus and the diploicin chemosyndrome. Based on these characteristics, a recent amendment of the genus by Bungartz *et al.* (2016) included species with either lecideine or lecanorine apothecia. The genus *Physcia* (Schreb.) Michx. (*Physciaceae*), with c. 75 accepted species, is characterized by a foliose thallus, a paraplectenchymatous upper cortex, and atranorin as the cortical substance (Moberg 1990; Elix 2011).

Materials and Methods

Study area

Specimens were collected from the tropical dry forest of the Chamela-Cuixmala Biosphere Reserve, located 2 km inland from the Pacific Coast of Mexico (20°N, 105°W). The reserve contains abundant and diverse lichen communities dominated by the

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families *Arthoniaceae*, *Graphidaceae* and *Pyrenulaceae* (Herrera-Campos *et al.* 2019; Miranda-González & McCune 2020). Detailed descriptions of the study area are found elsewhere (Noguera *et al.* 2002; Maass *et al.* 2018).

Anatomical studies

Specimens were studied using standard techniques with a Zeiss Stemi DV4 dissecting microscope and a Euromex iScope compound microscope connected to an AmScope MU1803 digital camera. Thallus images were taken with a Nikon D5300 digital camera and a Leica Z16 APOA dissecting microscope connected to a Leica DFC490 camera using the software Leica Application Suite v. 4.3.0. Sections and all anatomical measurements were made on material mounted in tap water. Thin-layer chromatography (TLC) was performed in solvents A and C using the standard techniques outlined in Elix (2014) and McCune (2017). *Diploicia canescens* (Dicks.) A. Massal. was used as a control for the identification of secondary metabolites.

Taxon sampling for molecular analyses

We performed two sets of phylogenetic analyses, one for *Diploicia* and one for *Physcia*. For the *Diploicia* analyses, taxon sampling included all available sequences in GenBank of *Diploicia*, selected sequences of the closely related *Diplotomma* Flot., and selected sequences of *Pyxine* Fr. which was used as outgroup following Helms *et al.* (2003), Prieto & Wedin (2017) and Ai *et al.* (2022). Datasets were selected using data from Grube & Arup (2001), Bhattacharya *et al.* (2002), Molina *et al.* (2002), Nadyeina *et al.* (2010), Prieto & Wedin (2017), Yang *et al.* (2018), Moya *et al.* (2020), Wang *et al.* (2020) and Ai *et al.* (2022), together with new sequences generated in this study (Supplementary Material Table S1, available online). A second analysis for *Diploicia* (Supplementary Material Fig. S1, available online) included all available ITS sequences of *Diplotomma* and was carried out to ensure the separation of the genera *Diploicia* and *Diplotomma*. For the *Physcia* analyses, we selected a monophyletic clade from Esslinger *et al.* (2020) that contained our new species, along with the sister clade containing *Physcia jackii* Moberg as outgroup; from there, we undertook taxon sampling and chose datasets from Helms *et al.* (2003), Elix *et al.* (2009), Orock *et al.* (2012), Ohmura *et al.* (2020), Rangsiruji *et al.* (2020), Miranda-González *et al.* (2023), and the new sequences generated in this study (Supplementary Material Table S1).

DNA extraction, PCR and sequencing

For each sample, a piece of thallus *c.* 2 mm diam. was detached and washed in acetone for 5 min at 70 °C, followed by two more acetone washes at room temperature. Genomic DNA was isolated using the Sigma-Aldrich REDExtract-N-Amp Plant PCR Kit following the manufacturer's instructions, except only 15 µl of extraction buffer and 15 µl of dilution buffer were used per sample. The whole ITS and portions of mtSSU and nuLSU were amplified and sequenced using the following primers: ITS1F/ITS4 (White *et al.* 1990; Gardes & Bruns 1993), mrSSU1/mrSSU3R (Zoller *et al.* 1999), and AL2R/LR6 (Vilgalys & Hester 1990; Mangold *et al.* 2008).

Amplifications were performed with 10 µl PCR reactions consisting of 5 µl R4775 Sigma-Aldrich REDExtract-N-Amp PCR Ready Mix, 0.5 µl of each primer (10 µM), 3 µl water, and 1 µl

diluted DNA template. The PCR cycling conditions for ITS were as follows: 95 °C for 5 min, followed by 35 cycles of 95 °C for 30 s, 52 °C for 45 s, and 72 °C for 105 s, followed by 72 °C for 5 min. The PCR cycling conditions for mtSSU and nuLSU were: 95 °C for 5 min, followed by 35 cycles of 95 °C for 1 min, 53 °C (for mtSSU) or 57 °C (for nuLSU) for 1 min, and 72 °C for 105 s, followed by 72 °C for 10 min. PCR products (2 µl per sample) were visualized on 1.5% TBA agarose gel stained with GelRed (Biotium, San Francisco, CA, USA). PCR products were purified using ExoSAP-IT (ThermoFisher, Waltham, MA, USA) before Sanger sequencing.

Molecular work, including sequencing, was carried out at the Laboratorio de Biología Molecular, as part of the Laboratorio Nacional de Biodiversidad, in the Instituto de Biología of the Universidad Nacional Autónoma de México.

Phylogenetic analysis

New sequences were edited in Geneious R11 (Kearse *et al.* 2012). All sequences from each genetic marker were aligned independently with MAFFT (Katoh & Standley 2013) and manually corrected. For the genus *Diploicia*, we included the genetic markers ITS and mtSSU in the phylogenetic analyses. For the genus *Physcia*, we included only ITS because the genetic markers mtSSU and nuLSU are not well represented in GenBank; however, all three genetic markers were obtained from the holotype. The final concatenated alignments are available as Supplementary Material Files S1 and S2 (available online). The maximum likelihood (ML) analyses of all markers, partitioned by marker, were performed using RAxML v. 8.2.11 (Stamatakis 2014), with 550 bootstrapping replicates. The Bayesian analyses were performed using MrBayes v. 3.2.6 (Ronquist *et al.* 2012), with one million generations and default settings. All analyses were performed with the GTR GAMMA I model and run on Geneious R11. The final ML trees were plotted in Geneious R11 and edited in Photoshop.

Results and Discussion

Phylogenetic analyses

This study generated a total of 10 sequences (Table 1). The dataset for the *Diploicia* analyses consisted of 1378 unambiguously aligned characters, 540 from ITS and 838 from mtSSU, of which 275 and 202, respectively, were phylogenetically informative. The dataset for the *Physcia* analyses consisted of 530 unambiguously aligned characters, of which 197 were phylogenetically informative.

As previously shown by Molina *et al.* (2002), our phylogenetic analyses for *Diploicia* (Fig. 1) resolved the genus as monophyletic. However, contrary to Molina *et al.* (2002) and in agreement with subsequent studies, we believe that *Diploicia* should not be synonymized with *Diplotomma*, but rather be considered as its sister group. This conclusion is supported by their different growth form which is correlated with a clear separation in the phylogenetic analysis (Supplementary Material Fig. S1, available online). The new species *Diploicia edulis*, described below, provides the first molecular evidence to include species with lecanorine apothecia in the genus, an amendment proposed by Bungartz *et al.* (2016) based on morphological and chemical evidence, that also occurs in the closely related genus *Pyxine*. Molina *et al.* (2002) suggested that the sorediate species *Diploicia*

Table 1. GenBank Accession numbers of new sequences generated in this study. – indicates missing data. * indicates holotypes. All samples are from Mexico (all specimens are deposited in MEXU).

| Species | Voucher | Isolate | ITS | mtSSU | nuLSU |
|-------------------------------|---|---------|----------|----------|----------|
| <i>Diploicia edulis</i> * | R. Miranda-González 6011 | RMG 407 | PQ137213 | PQ137209 | – |
| <i>Physcia ornamentalis</i> * | R. Miranda-González 5029 | RMG 353 | PQ137214 | PQ137210 | PQ137218 |
| <i>P. ornamentalis</i> | R. Miranda-González 1124 | RMG 613 | PQ137212 | – | – |
| <i>P. ornamentalis</i> | R. Miranda-González 5102 | RMG 458 | PQ137215 | – | – |
| <i>P. ornamentalis</i> | R. Miranda-González 5111 | RMG 465 | PQ137216 | – | – |
| <i>P. ornamentalis</i> | R. Miranda-González 5131 | RMG 464 | PQ137217 | – | – |
| <i>P. ornamentalis</i> | M. A. Herrera-Campos et al. 2008 288-58 | RMG 597 | PQ137211 | – | – |

canescens and the fertile species *D. subcanescens* (Werner) Hafellner & Poelt should be synonymized; however, as shown in many other lichen groups, our phylogenetic results suggest that the widely distributed *D. canescens* is a species complex that needs further revision. Similarly, sequenced species of *Diplotomma* show further work is required in many cases to define monophyletic species (Supplementary Material Fig. S1).

Our phylogenetic analyses for *Physcia* resolved the new species *Physcia ornamentalis*, described below, and the morphologically similar *P. undulata* Moberg in related but different clades (Fig. 2). Instead, *P. ornamentalis* was resolved next to a clade of Australian species that differ morphologically by the patterns of soralia present.

Taxonomy

Diploicia edulis R. Miranda, Campos-Cerda & Herrera-Camp. sp. nov.

MycoBank No.: MB 855034

Similar to *Diploicia endopyxinea* (Müll. Arg.) Kalb *et al.* but differs by having a subhymenium conspicuously interspersed with oil droplets, a greyish thallus surface, epruinose apothecia, and a neotropical distribution (Mexico).

Type: Mexico, Jalisco, La Huerta Mun., Chamela-Cuixmala Biosphere Reserve, Estación de Biología Chamela, on Chachalacas trail, tropical dry forest, 19°29'49"N, 105°2'35"W, alt. 90 m, on a canopy branch of a fallen tree, August 2015, R. Miranda-González 6011 (MEXU—holotype). GenBank Accession nos.: PQ137213 (nuITS), PQ137209 (mtSSU).

(Fig. 3)

Thallus corticolous, subfoliose, placodioid, orbicular or irregularly spreading, tightly adnate to the substratum, up to 4 cm wide. *Lobes* up to 1 mm wide, convex to slightly plane, branching irregular to anisotomic, mostly contiguous, sometimes imbricate and rarely discrete at the apices, margin entire, apices truncate to rounded. *Central areoles* continuous, convex to bullate, abundantly covered by pycnidia and apothecia. *Upper surface* whitish grey, dull, pruina sometimes present in small amounts at the lobe apices. *Soralia* absent. *Upper cortex* paraplectenchymatous. *Medulla* white throughout.

Apothecia common, clearly lecanorine with lecideine stage in young apothecia not observed, up to 1.2 mm wide, sessile, flat; *disc* black, epruinose, lower than the thalline margin; thalline margin frequently crenulate, same colour as the thallus, with

cortex, photobiont layer, and medulla; *proper exciple* reduced and hyaline in mature apothecia, light brown towards the hypothecium; *epihymenium* dull brown, not diffused by a green pigment (K–); *hymenium* hyaline, not interspersed; *subhymenium* hyaline to light brown at the edge of the hypothecium, conspicuously interspersed with oil droplets; *hypothecium* light brown, extending further than the proper exciple into a short stipe. *Asci* clavate, 8-spored. *Ascospores* 1-septate, grey-brown to darker brown when old, smooth, narrowly ellipsoid, with slightly pointed ends, with distinct apical thickenings of a lighter colour; cell lumina initially angular but soon thin-walled (*Dirinaria*-type), 10–14 × 4–6 µm (*n* = 21).

Pycnidia abundant, immersed, flask-shaped. *Conidia* hyaline, simple, bacilliform, not tapered at ends, 4–6 × 0.7–1.2 µm (*n* = 15).

Chemistry. TLC shows atranorin, diploicin and an accessory substance related to diploicin. Spot test: K+ yellow and P+ yellow on cortex, all other reactions negative.

Etymology. The epithet *edulis* ('edible' in Latin) has been chosen to emphasize that specimens of the new species frequently appear damaged, showing feeding traces as a result of invertebrate herbivory.

Ecology and distribution. The new species is so far known only for the tropical dry forest of the Chamela-Cuixmala Biosphere Reserve in Jalisco, Mexico. It is a rare species associated with canopy branches. All known specimens show signs of invertebrate consumption.

Remarks. The new species resembles *Diploicia endopyxinea*, an endemic to Socotra, Yemen, that differs by its pale white surface, apothecia with weakly pruinose discs, and subhymenium without oil droplets. *Diploicia glebosa* (Tuck.) Bungartz *et al.* and *D. neotropica* Kalb *et al.*, two saxicolous species endemic to the Galapagos Islands, differ by their olivaceous epihymenium that reacts K+ faintly violet and by their larger ascospores (Bungartz *et al.* 2016). All other species in the genus have lecideine apothecia. *Diploicia edulis* will key out in couplet 5 of Bungartz *et al.* (2016) as: 'Epihymenium pale to dull brown, without a diffuse green pigment (K–); apothecia with black epruinose discs, subhymenium with oil droplets; known only from the Pacific coast of Mexico.'

Additional specimens examined (paratypes). Mexico: Jalisco: La Huerta Mun., Chamela-Cuixmala Biosphere Reserve, Estación de Biología Chamela, on Chachalacas trail, tropical dry forest, alt.

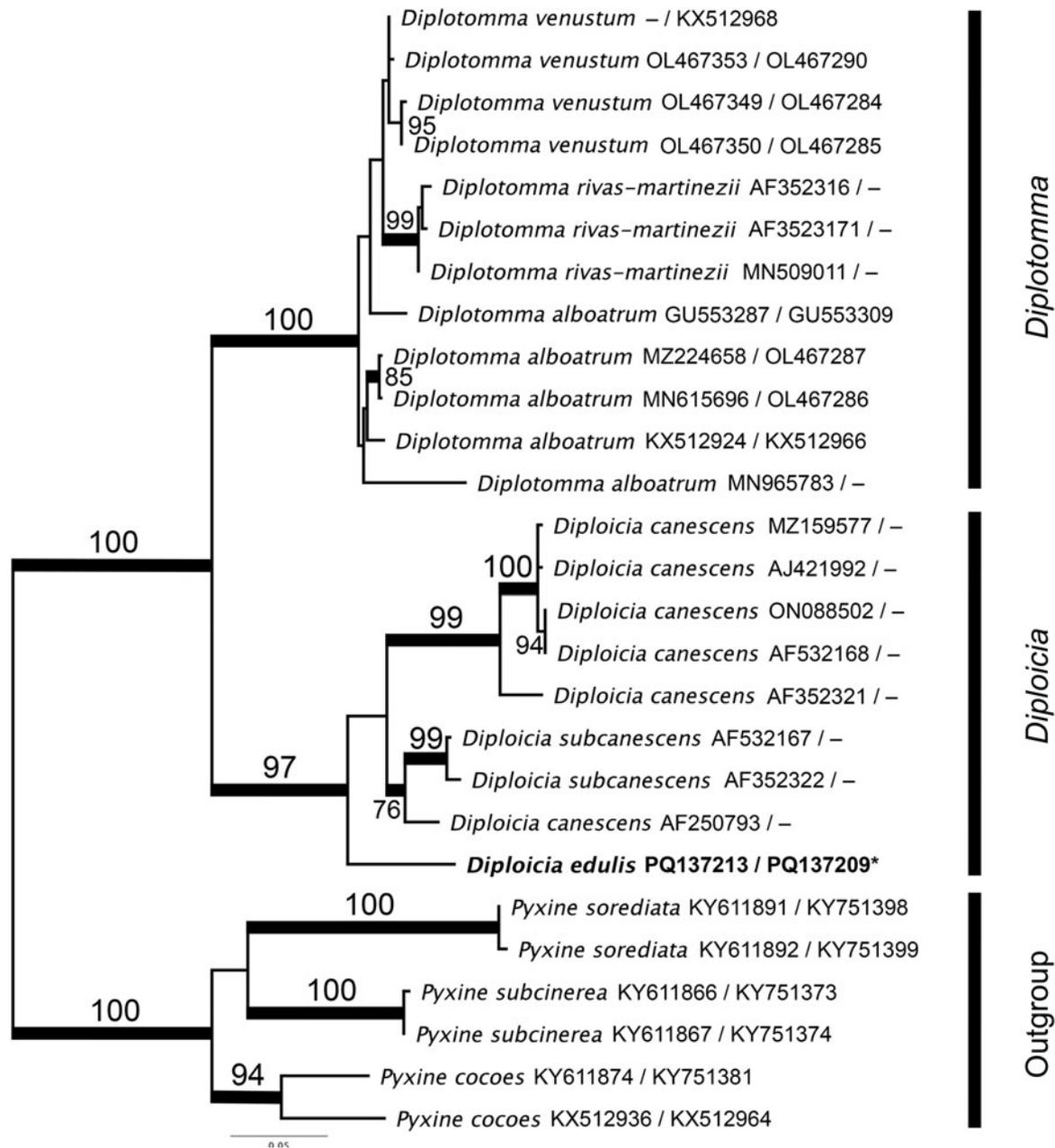


Figure 1. Phylogeny of the genus *Diploicia* based on a maximum likelihood (ML) analysis of the genetic markers nuITS and mtSSU. Support values are shown as numbers if ML bootstrap values are ≥ 70 and as bold branches if Bayesian posterior probabilities are ≥ 0.95 . Bold names show new sequences from this study and * indicates sequences from the type collection. The name of each terminal branch includes GenBank numbers of nuITS/mtSSU with – indicating missing data.

90 m, on a canopy branch of a fallen tree, 2015, R. Miranda-González 5208 (MEXU), 6012 (MEXU).

***Physcia ornamentalis* R. Miranda, Campos-Cerda & Herrera-Camp. sp. nov.**

Mycobank No.: MB 855035

Similar to *Physcia undulata* but differs by having soralia originating from the lobe sinuses and by lacking soralia in the thalline margin of the apothecia.

Type: Mexico, Jalisco, La Huerta Mun., Chamela-Cuixmala Biosphere Reserve, Estación de Biología Chamela, on Tejón trail, 1080 m, tropical dry forest, 19°30'30"N, 105°2'55"W, alt. 50 m, on a

canopy branch of a fallen tree, December 2015, R. Miranda-González 5029 (MEXU—holotype). GenBank Accession nos.: PQ137214 (nuITS), PQ137210 (mtSSU), PQ137218 (nuLSU).

(Fig. 4)

Thallus corticolous, orbicular or irregularly spreading, adnate to loosely adnate, up to 6 cm wide. *Lobes* up to 2 mm wide, plane to slightly convex, irregularly branched, discrete when young, and commonly imbricate in older thalli; margin entire to crenate, sometimes slightly raised; apices rounded to truncate. *Upper surface* grey bluish when young and later grey, dull, frosted-pruinose throughout, but the pruina often disappearing in the centre of older thalli. *Soralia* frequent and abundant, but not always present, originating from

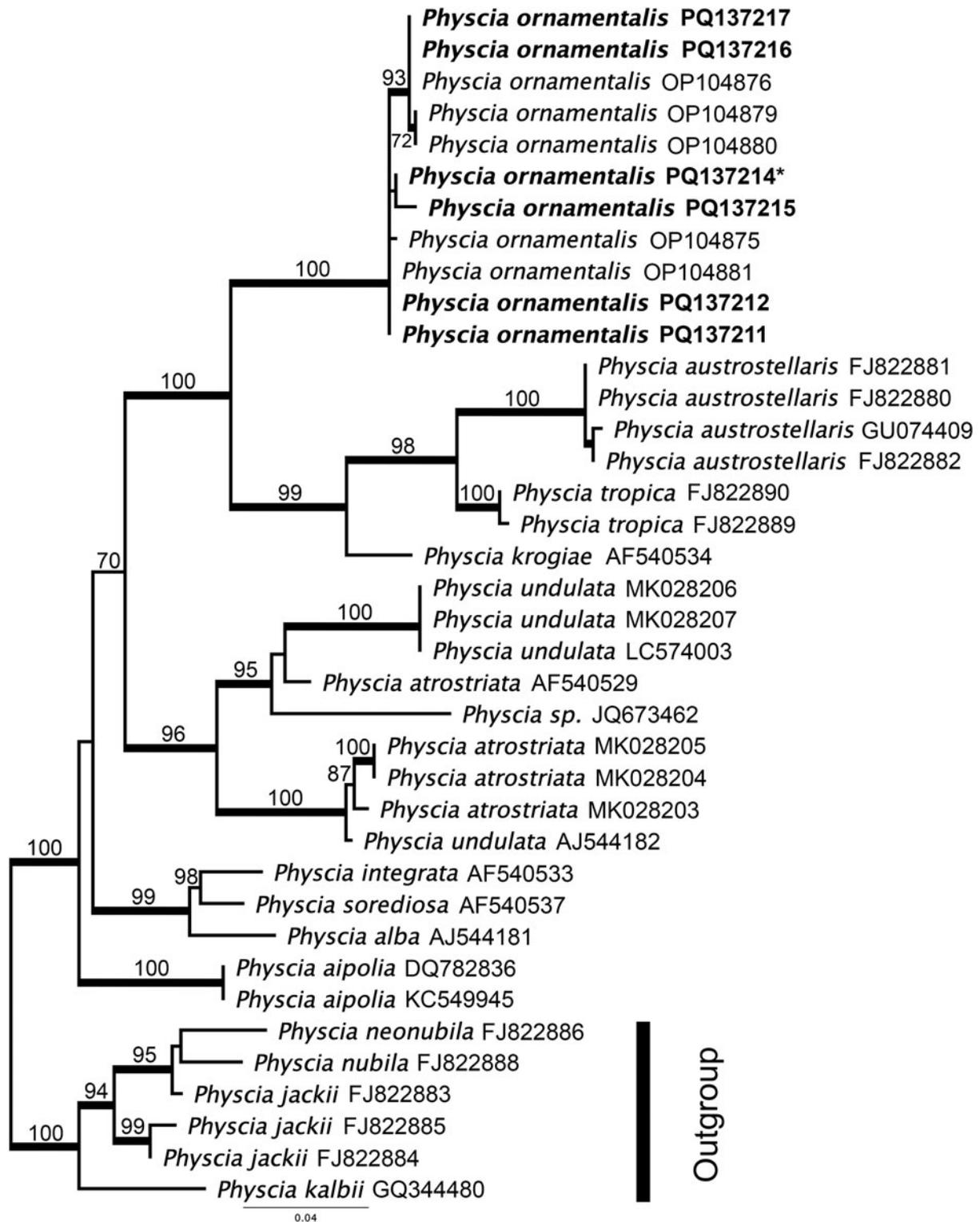


Figure 2. Phylogeny of selected *Physcia* species based on a maximum likelihood (ML) analysis of the genetic marker nuITS. Support values are shown as numbers if ML bootstrap values are ≥ 70 and as bold branches if Bayesian posterior probabilities are ≥ 0.95. Bold names show new sequences from this study and * indicates sequences from the type collection. The name of each terminal branch includes GenBank numbers of nuITS.

the lobe sinuses at the centre of the lobes, soralia appearing as laminal or marginal if lobe sinuses get concealed with the growth of the thalli; on the centre of old thalli soralia appearing as almost labiate. Lower surface whitish to pale brown; rhizines white to black, sparse, denser at the margins, simple with a squarrose tuft at the tip. Upper cortex paraplectenchymatous, lower cortex mostly resembling

a paraplectenchyma although cells are not always rounded or angular and hyphae can occasionally still be distinguished.

Apothecia common, 0.5–2.5 mm wide, sessile, convex in larger apothecia; margin persistent, not sorediate; disc light brown, not pruinose, lower than the thalline margin. *Ascospores* intermediate between *Pachysporaria* and *Physcia*-type, 20–25 × 10–12.5 μm.

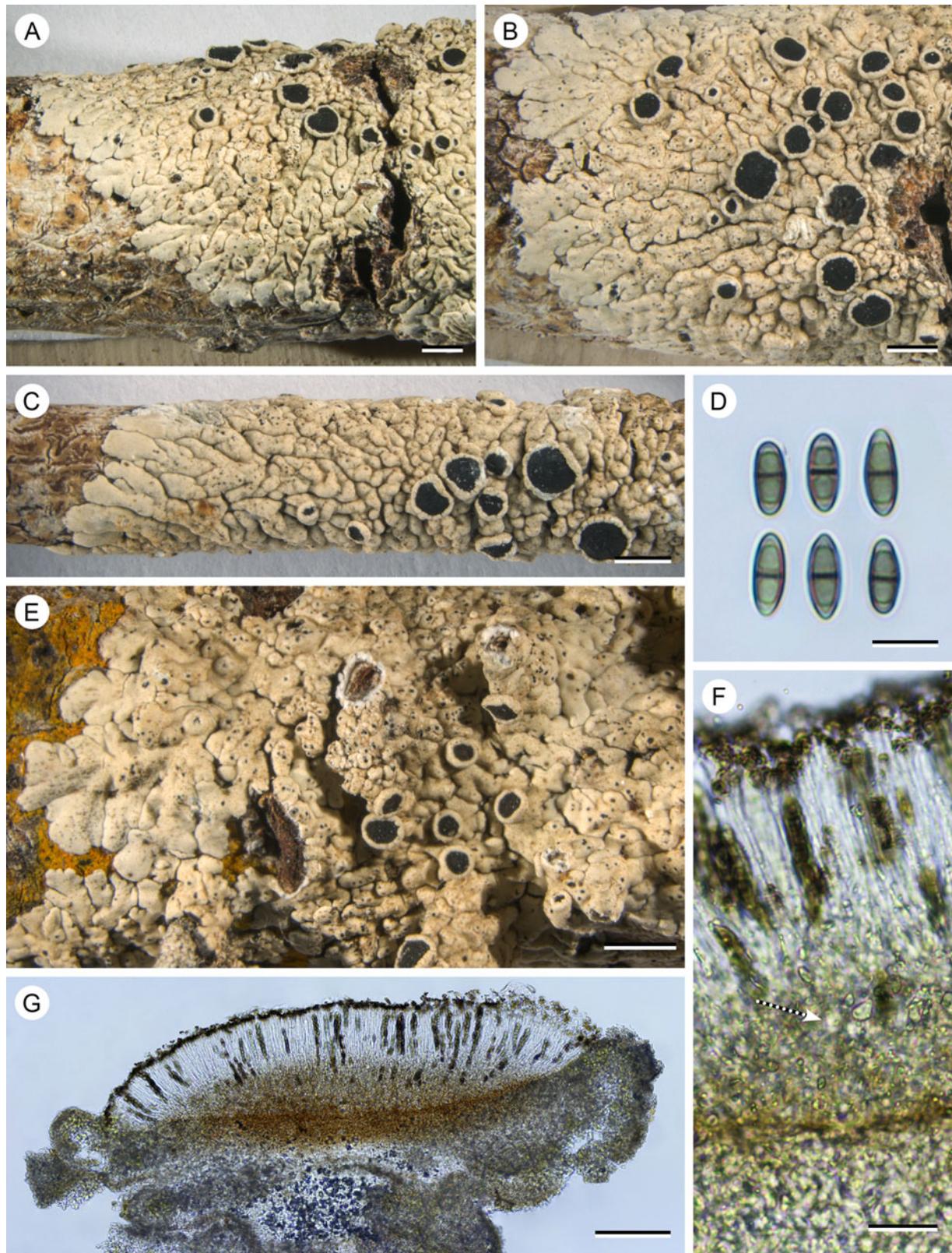


Figure 3. *Diploicia edulis*. A–C & E, habit showing placodioid thalli, lecanorine apothecia and abundant pycnidia. D, *Dirinaria*-type ascospores. F, subhymenium treated with KOH and showing abundant oil droplets (arrow). G, section of a mature apothecium. A, B, D, F & G, *R. Miranda-González* 6011 (holotype, MEXU). C, *R. Miranda-González* 5208 (MEXU). E, *R. Miranda-González* 6012 (MEXU). Scales: A–C & E = 1 mm; D = 5 μ m; F = 20 μ m; G = 100 μ m. In colour online.

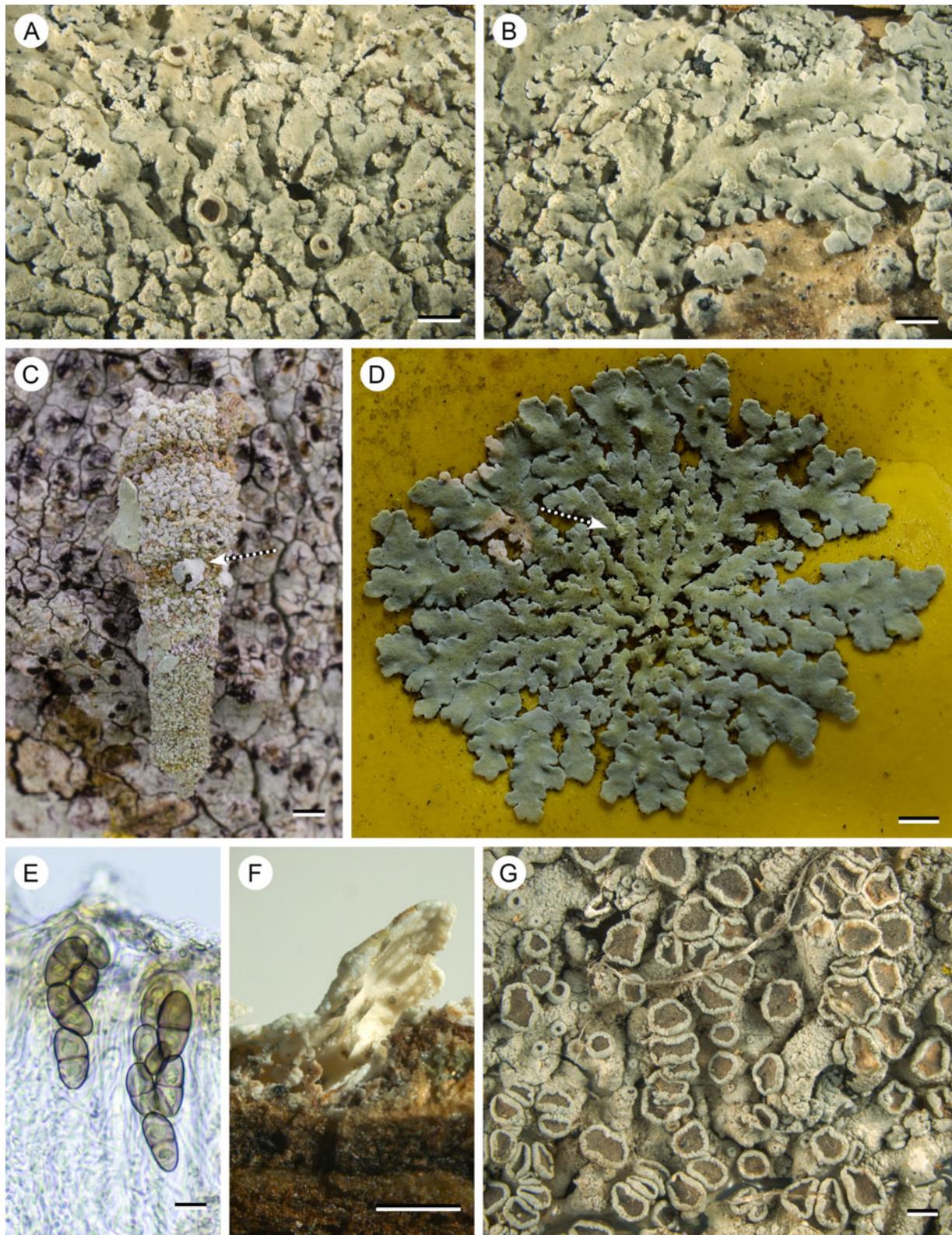


Figure 4. *Psychia ornamentalis*. A & B, habit showing thallus with abundant pruina, apothecia and soralia. C, *in situ* use of *P. ornamentalis* (arrow) for bag construction by a *Psychidae* caterpillar. D, young thallus growing on a piece of flagging showing soralia originating from the lobe sinuses (arrow). E, ascospores showing an intermediate form between *Psychia* and *Pachysporaria*-type. F, lower surface uniformly white. G, old thallus showing abundant apothecia and lacking soralia. A, B, E & F, R. Miranda-González 5029 (holotype, MEXU). C, R. Miranda-González 18-2 (MEXU). D, F. Campos-Cerda s. n. (MEXU); G, M. A. Herrera-Campos et al. 2008 288-58 (MEXU). Scales: A–D & G = 1 mm; E = 10 μ m; F = 0.5 mm. In colour online.

Chemistry. TLC results show atranorin, zeorin and several other unknown triterpenes. Spot test: K⁺ yellow on cortex and medulla, all other reactions negative.

Etymology. The epithet refers to the use of this species by *Psychidae* caterpillars to construct their bags.

Ecology and distribution. The new species is so far known only from the tropical dry forest in and around the Chamela-Cuixmala Biosphere Reserve in Jalisco, Mexico. It was found associated with *Bursera* sp., *Erythrina lanata* and several other unidentified trees, both at the understorey and the canopy. *Physcia ornamentalis* was also found growing on old flagging, and most notably, it was one of the main materials used by *Psychidae* caterpillars in the construction of their bags, as noted by Miranda-González et al. (2023) and identified in that paper as *Physcia undulata* s. lat. The presence of triterpenes might explain the high use of *P. ornamentalis* as bag material by *Psychidae* caterpillars, given that such compounds often display antimicrobial properties (Jasso de Rodríguez et al. 2006; Mateos-Maces et al. 2020) and nests and refuges are important elements involved in the early colonization and regulation of microbiome assembly in developing animals (Campos-Cerda & Bohannan 2020).

Remarks. In one sequenced specimen (Herrera-Campos et al. 288–58), the thallus was abundantly covered with apothecia, but no soralia were found; nonetheless, the phylogenetic analysis confirms that both forms are the same species. *Physcia ornamentalis* will key out as *Physcia undulata* in most of the available keys around the world; however, it differs morphologically by having soralia originating in the lobe sinuses instead of in the lobe margins and by lacking soralia in the thalline margin of the apothecia. *Physcia undulata* was described from a small number of collections from Kenya and Ethiopia (Moberg 1986), and soon after it was reported for several places around the world, such as the Americas (Moberg 1990) and Australia (Elix 2011). According to Moberg (1990), the significant variability throughout its distribution, in thallus and ascospore size, suggests that *P. undulata* is probably a species complex. *Physcia ornamentalis* is phylogenetically close to a clade of Australian species including *Physcia austrostellaris* Elix., *P. krogiae* Moberg and *P. tropica* Elix (Fig. 2). Of these, the only species with a frosted-pruinose appearance is *P. krogiae* which differs from the new species by having laminal pustulate soralia. *Physcia ornamentalis* will key out in couplet 16 of Moberg (1990) as: ‘Soralia originating from the lobe sinuses, ‘frosted’ at least along margins.’

Additional specimens examined. **Mexico:** Jalisco: La Huerta Mun., Chamela-Cuixmala Biosphere Reserve, Estación de Biología Chamela, on Chachalacas trail, tropical dry forest, alt. 90 m, on bark of unknown trees, 2008, M. A. Herrera Campos et al. 2008 288–58 (MEXU), 2009, R. Miranda-González 1124 (MEXU), 2014, R. Miranda-González 4539 (MEXU); *ibid.*, on Calandria trail, tropical dry forest, alt. 126 m, on bark of unknown tree, 2011, A. Barcenás Peña 4410 (MEXU); *ibid.*, on Tejón trail, tropical dry forest, alt. 50 m, on old flagging attached to a tree, 2015, F. Campos-Cerda s. n. (MEXU); *ibid.*, on bark of unknown tree, 2019, R. Miranda González 5111 (MEXU).

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Competing Interests. The authors declare none.

Data Accessibility. Newly generated sequences have been deposited in GenBank. Nomenclatural novelties have been deposited in MycoBank.

Supplementary Material. The Supplementary Material for this article can be found at <https://doi.org/10.1017/S0024282925000015>.

Supplementary File S1. Concatenated alignment of the genetic markers nuITS and mtSSU used for the phylogenetic analyses of the genus *Diploicia*.

Supplementary File S2. Concatenated alignment of the genetic marker nuITS used for the phylogenetic analyses of selected species of *Physcia*.

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