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The lichenized genus *Cora* (*Basidiomycota*: *Hygrophoraceae*) in Mexico: high species richness, multiple colonization events, and high endemism

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Article info

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Associate Editor Adam Flakus Abstract. In a continued effort to catalog the numerous phylogenetically detected and predicted species of Cora in the Americas, we focus here on the diversity of the genus in Mexico and the phylogenetic relationships of the taxa present in this area. Based on previous results and new collections, 12 taxa are recognized in Mexico, including eight new species and one new subspecies. The 12 taxa form 11 unrelated lineages within the genus, indicating multiple independent colonization from Central and South America. While the new subspecies is nested within a species known from the northern Andes in South America, the other species are all putative endemics for Mexico, resulting in endemism of 92% at species level and 100% at taxon level. Considering the rather narrow area of origin of the sequenced specimens in southeastern Mexico and the previously documented range of Cora including the northwestern part of the country, plus the underlying topography, we predict that the 12 species and subspecies now known represent only about 20% of the total richness of Cora in the country, and that many more endemic lineages are to be found in the western and northwestern parts (Sierra Madre Occidental). The new taxa from Mexico formally introduced in this study are Cora benitoana sp. nov., with a strongly projecting, cyphelloid hymenophore; C. buapana sp. nov., with elongate, finger-like and partly branched appendages on the lower medullary hyphae; C. dewisanti subsp. mexicana subsp. nov., with a marginally protruding hymenophore; C. guzmaniana sp. nov., with a partly setose lobe surface; C. ixtlanensis sp. nov., a phenotypically cryptic species similar but unrelated to C. terrestris; C. lawreyana sp. nov., with globose hyphal appendages; C. marusae sp. nov., a phenotypically cryptic species similar but unrelated to C. comaltepeca; C. totonacorum sp. nov., a phenotypically cryptic species similar but phylogenetically distant to C. davidia; and C. zapotecorum sp. nov., with a very thinly pilose lobe surface.

Key words: Cora casasolana, Cora comaltepeca, Cora dulcis, Frullania, Rhizonema, Central Volcanic Belt, Isthmus of Tehuantepec, Sierra Madre de Chiapas, Sierra Madre Oriental

Introduction

With a share of about 1%, Basidiomycota form only a small proportion of all lichenized fungi (Lücking et al. 2017a). However, the genus *Cora*, until recently believed to comprise only a single species (Parmasto 1978; Chaves et al. 2004), has been shown to be hyperdiverse, with nearly 200 species already detected using ITS barcoding, 93 of which have so far been formally described, and over 450 species predicted (Lücking et al. 2013, 2014, 2017b). Although *Cora* has been demonstrated to occur on islands in the South Atlantic, in tropical Africa and in Asia (Lücking et al. 2015, 2017b), over 95% of the known species are restricted to the Americas, the genus being most diverse in the northern Andes but also found as far north as Mexico and Florida, and as far south as southern Chile (Lücking et al. 2014, 2017b).

The occurrences of *Cora* in Mexico and Florida mark the northernmost distribution of the genus, which is remarkable, given that the latitudinal distribution range of *Cora* reaches only 28° north in Mexico and Florida but 40° south in southern Chile, a difference of more than 1300 km. The reasons for the absence of *Cora* in western

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North America north of Mexico are unknown. For Mexico, until recently only a single species had been reported, under the names C. glabrata, C. pavonia, Dictyonema glabratum and D. pavonium (Imshaug 1956; Ryan et al. 1996; García et al. 2000; Guzmán 2008; Lücking et al. 2009). The first sequence data for a Mexican specimen were published by Lücking et al. (2009, 2014) as D. glabratum and Dictyonema sp., respectively. After the formal recognition of Cora as a genus separate from Dictyonema s.str. (Dal Forno et al. 2013; Lücking et al. 2013), a much broader sampling of Cora revealed the presence of at least nine lineages in Mexico, none of them conspecific with C. glabrata s.str. or C. pavonia s.str., two species likely endemic to the Caribbean (Lücking et al. 2013, 2015). Thus far, three new species from Mexico have been formally described: C. casasolana, C. comaltepeca and C. dulcis. A further lineage was found nested within C. dewisanti, a species known from the northern Andes in Colombia, Venezuela and Ecuador (Lücking et al. 2017b).

For the present study we included additional material from Mexico to reassess the diversity and evolutionary origins of this genus at its northernmost western limit in the Americas. We present an updated phylogeny based on the fungal ITS barcoding marker, revealing 12 distinct lineages, eight of which are formally introduced as new species and one as new subspecies in this paper.

Material and methods

Fresh material of *Cora* was collected in Mexico by the first two authors between 2015 and 2017 in the states of Oaxaca and Veracruz. Specimens were studied at the Botanical Garden and Botanical Museum (Berlin, Germany), using standard techniques of light microscopy and thin-layer chromatography (Orange et al. 2010). We employed a standardized protocol for morphological, anatomical and chemical characters to characterize the material (Lücking et al. 2013, 2017b; Vargas et al. 2014). Voucher specimens were deposited at EB-BUAP, with duplicates at B.

Part of the material had already been sequenced to provide the framework for an earlier, large-scale taxonomic paper in which three species from Mexico were also formally described (Lücking et al. 2017b). In addition to the 36 already published ITS sequences in that study, here we generated a further 18 new ITS sequences, following previously published protocols (Dal Forno et al. 2013; Lücking et al. 2017c). The newly generated sequences were added to the global dataset of 653 sequences (including two outgroup taxa) assembled in the previous study (Lücking et al. 2017b), for a total of 671 sequences (Table 1, Table S1), and were manually aligned (File S1) after checking their position using the local blast function in BioEdit 7 (Hall 1999). The dataset was subjected to a maximum likelihood search using RAxML 8.2.8 on the CIPRES Science Gateway server (Miller et al. 2010; Stamatakis 2015), with non-parametric bootstrapping using 402 replicates (automatically determined based on a saturation criterion) under the universal GTR-GAMMA model.

To place the sequenced collections from Mexico into a broader context allowing assessment of the sampling effort, we assembled a database of known occurrences of *Cora* from Mexico from CNALH (https://lichenportal. org/cnalh) and GBIF (https://www.gbif.org), searching under the names *C. glabrata*, *C. pavonia*, *D. glabratum* and *D. pavonium* (Table S2). All collections were then mapped using Map Maker (https://www.darrinward.com/ lat-long).

Results and discussion

Phylogeny. The best-scoring maximum likelihood tree matches the topology obtained by Lücking et al. (2017b), dividing *Cora* into two large, well-supported clades, clade I and clade II (96% and 100% bootstrap support, respectively; Fig. 1, Fig. S1). The Mexican specimens form 12 lineages, all except two unrelated to each other and more or less evenly distributed over the tree, with three lineages in clade I and nine in the larger clade II (Fig. 1, Fig. S1). Eight represent new species and one a new subspecies, all formally described below.

Five lineages are represented by singletons (*C. casasolana*, *C. comaltepeca*, *C. dulcis*, *C. lawreyana*, *C. totonacorum*), whereas seven lineages (*C. benitoana*, *C. buapana*, *C. dewisanti* subsp. *mexicana*, *C. guzmaniana*, *C. ixtlanensis*, *C. marusae*, *C. zapotecorum*) contain between two and 16 specimens each (Table 1, Fig. S1). Of the non-singleton lineages, seven are reciprocally monophyletic, whereas one is nested within a known species, *C. dewisanti* (Fig. S1). The two Mexican lineages *C. cacasolana* and *C. totonacorum* (both singletons) form a sister clade (Fig. S1), thus resulting in 11 independent lineages present in Mexico (Fig. 1).

The closest relatives of these 11 Mexican lineages are in four cases species from Costa Rica, in six cases species from Colombia and adjacent areas in the northern Andes (Venezuela, Ecuador), and in one case unresolved (Fig. S1). The Mexican species with Costa Rican relatives are *C. marusae* (with *C. minor* and *C. paraminor*), *C. benitoana* (with *C. barbulata*), *C. casasolana* and *C. totonacorum* (with *C. haledana*), and *C. ixtlanensis* (with *C. terrestris*; Fig. S1).

Phenotype characters. Including the aforementioned species, eight of the 12 Mexican taxa can be compared in their phenotype characters (see descriptions and key below) directly to closely related and phenotypically characterized species (Fig. S1; see also Ariyawansa et al. 2015; Lücking et al. 2017b). Thus, C. marusae (Mexico) agrees with C. minor and C. paraminor (both Costa Rica) in the epiphytic growth, small size, and formation of soredia, but differs in the presence of papilliform hyphal appendages on the lower medullary hyphae and in the forest-green rather than olive-green fresh color. Cora benitoana (Mexico) and C. barbulata (Costa Rica) share the epiphytic growth habit and the cyphelloid hymenophore, as well as the absence of papilliform hyphal appendages on the lower medullary hyphae, but differ in habitat ecology (forest vs. paramo), size (medium-sized vs. large), surface



Figure 1. Circular cladogram of the genus *Cora* (outgroup *Corella*) based on 669 ITS ingroup OTUs, showing the phylogenetic position of specimens from Mexico (orange). For the full tree with terminal labels and branch support, see Fig. S1.

(glabrous vs. setose) and the formation of projecting, shortly stipitate basidiocarps in *C. benitoana*. The three species *C. casasolana*, *C. totonacorum* (both Mexico) and *C. haledana* (Costa Rica) agree in having medium-sized thalli and lobes with more or less greenish fresh color (olive-green to dark green) and the papilliform hyphal appendages on the lower medullary hyphae. However, they all differ in their substrate ecology, *C. casasolana* being terrestrial and the other two species epiphytic; *Cora totonacorum* can further be distinguished in the formation of soredia.

Cora ixtlanensis (Mexico) and *C. terrestris* (Costa Rica) both grow terrestrially, have medium-sized thalli and lobes with olive-grey color when fresh, share the corticioid hymenophore with concentric arrangement, and lack papilliform appendages on the lower medullary hyphae; both can be considered phenotypically cryptic species

but they are clearly distinct phylogenetically, differing consistently in five positions in the ITS (File S1). In the global ITS phylogeny (Fig. S1) they appear rather close, with *C. terrestris* receiving low support (62%) on a short branch, but the resolution and support within this terminal clade increase when analyzed separately (not shown). All species in this terminal clade, also including *C. caliginosa*, *C. auriculeslia*, *C. ciferrii*, *C. paraciferrii* and *C. squamiformis*, are terrestrial and very closely related, but differ partly in phenotype and substrate ecology, some growing directly on soil and others between grasses or bryophytes, and the species are largely allopatric, so this entire clade appears to represent a very recent radiation.

The sister-group relationship between *C. lawreyana* (Mexico) and *C. minutula* (Ecuador) is not supported and both form long branches, which may explain that the two are quite distinct phenotypically: medium-sized

Table 1. Voucher information and GenBank accession numbers for the Mexican specimens used in this study. Newly generated accessions are bolded. For GenBank accession numbers of the remaining, non-Mexican specimens used, see Table S1.

Genus	Species	ITS Accession	Country	Collectors	Number
Cora	benitoana	KX772550	Mexico	B. Moncada & RE. Pérez-Pérez	10193
Cora	benitoana	KX772555	Mexico	B. Moncada & RE. Pérez-Pérez	10180
Cora	benitoana	KX772557	Mexico	B. Moncada & RE. Pérez-Pérez	10306
Cora	benitoana	KX772561	Mexico	B. Moncada & RE. Pérez-Pérez	10199
Cora	benitoana	KX772567	Mexico	B. Moncada & RE. Pérez-Pérez	10207
Cora	benitoana	KX772606	Mexico	B. Moncada & RE. Pérez-Pérez	10183
Cora	buapana	KX772554	Mexico	B. Moncada & RE. Pérez-Pérez	10305
Cora	buapana	KX772571	Mexico	B. Moncada & RE. Pérez-Pérez	10197
Cora	casasolana	KX772540	Mexico	B. Moncada & RE. Pérez-Pérez	10257
Cora	comaltepeca	KX772556	Mexico	B. Moncada & RE. Pérez-Pérez	10233
Cora	dewisanti subsp. mexicana	EU825957	Mexico	R. S. Egan	17538
Cora	dewisanti subsp. mexicana	KX772538	Mexico	B. Moncada & RE. Pérez-Pérez	10300
Cora	dewisanti subsp. mexicana	KX772543	Mexico	B. Moncada & RE. Pérez-Pérez	10297
Cora	dewisanti subsp. mexicana	KX772544	Mexico	B. Moncada & RE. Pérez-Pérez	10228
Cora	dewisanti subsp. mexicana	KX772545	Mexico	B. Moncada & RE. Pérez-Pérez	10278
Cora	dewisanti subsp. mexicana	KX772548	Mexico	B. Moncada & RE. Pérez-Pérez	10195
Cora	dewisanti subsp. mexicana	KX772549	Mexico	B. Moncada & RE. Pérez-Pérez	10196
Cora	dewisanti subsp. mexicana	KX772552	Mexico	B. Moncada & RE. Pérez-Pérez	10301
Cora	dewisanti subsp. mexicana	KX772558	Mexico	B. Moncada & RE. Pérez-Pérez	10185
Cora	dewisanti subsp. mexicana	KX772559	Mexico	B. Moncada & RE. Pérez-Pérez	10302
Cora	dewisanti subsp. mexicana	KX772560	Mexico	B. Moncada & RE. Pérez-Pérez	10176
Cora	dewisanti subsp. mericana	KX772562	Mexico	B Moncada & R - E. Pérez-Pérez	10154
Cora	dewisanti subsp. mexicana	KX772563	Mexico	B Moncada & R - E. Pérez-Pérez	10322
Cora	dewisanti subsp. mexicana	KX772569	Mexico	B. Moncada & RF. Pérez-Pérez	10198
Cora	dulcis	KX772551	Mexico	B. Moncada & RE. Pérez-Pérez	10288
Cora	aureis	MN475936	Mexico	R _F Pérez-Pérez & D León-González	1325
Cora	guzmaniana	MN475948	Mexico	RE. Pérez-Pérez & D. León-González RE. Pérez-Pérez & D. León-González	1323
Cora	guzmaniana	MN475950	Mexico	RE. Pérez Pérez & D. León-González	1325
Cora	guzmaniana	MN475940	Mexico	\mathbf{R} - \mathbf{E} . For \mathbf{C} - \mathbf{F} - \mathbf{C} -	1320
Cora	guzmaniana	MN475941	Mexico	RE. Pérez Pérez & D. León-González	1329
Cora	guzmaniana	MN475941 MN475944	Mexico	RE. FEICZ-FEICZ & D. Leon-González	1330
Cora	guzmaniana	MN475029	Maxiao	RE. Pérez Pérez & D. León-González	1222
Cora	guzmaniana	MN475930	Maxiao	RE. Felez-Felez & D. Leon-González	1332
Cora	guzmaniana	WIN475945	Mexico	RE. Felez-Felez & D. Leon-Golizalez	1333
Cora	guzmaniana	WIN475945	Mexico	RE. Pérez-Pérez & D. León-Gonzalez	1334
Cora	guzmaniana	MIN475947	Mexico	RE. Perez-Perez & D. Leon-Gonzalez	1335
Cora	guzmaniana	NIN475942	Mexico	RE. Perez-Perez & D. Leon-Gonzalez	1330
Cora	guzmaniana	MIN475951	Mexico	RE. Perez-Perez & D. Leon-Gonzalez	133/
Cora	guzmaniana	MN475943	Mexico	RE. Perez-Perez & D. Leon-Gonzalez	1338
Cora	guzmaniana	MN475939	Mexico	RE. Perez-Perez & D. Leon-Gonzalez	1327
Cora	guzmaniana	MN475937	Mexico	RE. Pérez-Pérez & D. León-González	1326
Cora	guzmaniana	MN475946	Mexico	RE. Pérez-Pérez & D. León-González	1298
Cora	ixtlanensis	KX772539	Mexico	B. Moncada & RE. Pérez-Pérez	10264
Cora	ixtlanensis	KX772547	Mexico	B. Moncada & RE. Pérez-Pérez	10205
Cora	ixtlanensis	KX772565	Mexico	B. Moncada & RE. Pérez-Pérez	10293
Cora	lawreyana	MN475935	Mexico	RE. Pérez-Pérez & G. Aguila-Rodríguez	1168
Cora	marusae	KX772541	Mexico	B. Moncada & RE. Pérez-Pérez	10212
Cora	marusae	KX772542	Mexico	B. Moncada & RE. Pérez-Pérez	10319
Cora	marusae	KX772553	Mexico	B. Moncada & RE. Pérez-Pérez	10178
Cora	marusae	KX772564	Mexico	B. Moncada & RE. Pérez-Pérez	10316
Cora	marusae	KX772570	Mexico	B. Moncada & RE. Pérez-Pérez	10222
Cora	totonacorum	MN475934	Mexico	RE. Pérez-Pérez & G. Águila-Rodríguez	1189b
Cora	zapotecorum	KX772546	Mexico	B. Moncada & RE. Pérez-Pérez	10318
Cora	zapotecorum	KX772566	Mexico	B. Moncada & RE. Pérez-Pérez	10307
Cora	zapotecorum	KX772568	Mexico	B. Moncada & RE. Pérez-Pérez	10206

vs. small, with vs. without papilliform appendages on the lower medullary hyphae, and with a corticioid hymenophore vs. soredia. *Cora guzmaniana* (Mexico) and *C. galapagoensis* (Galapagos) agree in the epiphytic growth and medium-sized thallus and lobes, as well as in the concentrically arranged, corticioid hymenophore and the presence of papilliform appendages on the lower medullary hyphae, but the first species differs in the pigmented hyphal layers enclosing the photobiont layer and in the coralloid-spinulose appendages on the lower medullary hyphae. Finally, *Cora dewisanti* subsp. *mexicana* (Mexico) differs consistently from the nominal subspecies (known from Colombia, Venezuela and Ecuador) in the much larger thallus and lobes and in the often marginally protruding hymenophore.

Thus, while the new species shared certain phenotypical characters between closely related lineages, most of the novel taxa are diagnosable by at least one character, supporting their taxonomic recognition not only on molecular grounds. The only exceptions are the morphologically cryptic species *C. ixtlanensis* and *C. terrestris*.

Associations of lichen thalli with bryophytes. Notably, of the 54 sequenced specimens studied here, 43 were associated with liverwort mats of the genus Frullania (Fig. 2), either exclusively (14) or with further bryophyte taxa in between, and then usually with the Frullania species being dominant (see also descriptions below). It was recently shown that Frullania may act as a reservoir for the cyanobacterial photobiont Rhizonema (Cornejo & Scheidegger 2016), which is the photobiont present in Cora lichens and their relatives, as well as in several cyanobacterial ascolichens (Lawrey et al. 2009; Cornejo & Scheidegger 2016). Since Cora disperses predominantly by basidiospores which require de-novo symbiosis to form a new thallus, the notable association of Cora thalli with Frullania mats may be explained by the presence of non-lichenized Rhizonema colonies in these liverworts. A similar association was found in the related Acantholichen galapagoensis, which predominantly grows on thick epiphytic Frullania mats (Dal Forno et al. 2017). An alternative explanation would be for these associations to be opportunistic, given the ubiquity of Frullania mats in the habitats where most Cora species abound. This is contradicted by the observation that the frequently sorediate species, C. marusae, which does not require a new photobiont to propagate, was in only one out of five cases associated with Frullania mats and in the other cases with other bryophytes. These other bryophytes, usually mosses, do not develop water sacs or analogous structures with cyanobacteria. The difference in the association with Frullania mats in non-sorediate vs. sorediate taxa is statistically significant (Chi-Square test with Yates correction: $\chi = 16.6$, p < 0.001). We therefore hypothesize that also in the case of Cora, Frullania mats may act as a reservoir for Rhizonema to form thalli through relichenization. Examination of associated Frullania mats revealed the presence of a variety of cyanobacteria both on the stem and leaf surfaces and in the water sacs, but none unequivocally identifiable as Rhizonema.



Figure 2. Examples of thalli of various *Cora* specimens associated with *Frullania* mats. A – C. *lawreyana* (holotype, field image); B – C. *buapana* (isotype, rewetted); C – C. *dewisanti* subsp. *mexicana* (Moncada & Pérez-Pérez 10300, rewetted).

More sophisticated methods including next-gen sequencing are required to test this hypothesis.

Species richness and putative endemism. The 54 sequenced specimens mostly originate from southeastern Mexico, from the states of Veracruz and Oaxaca, with one specimen also from southwestern Mexico in the state of Jalisco (Fig. 3). Overall, *Cora* has been recorded mostly from this area, but also from northwestern, western, central and southeasternmost Mexico, from the states of Chihuahua, Sinaloa, Durango, Jalisco, México D.F., Puebla, Tlaxcala and Chiapas (Fig. 3). Thus, while the sequenced material chiefly represents the eastern coniferous and



Figure 3. Map showing recorded distribution of *Cora* in Mexico. Red circles: occurrence records from CNALH and GBIF; blue circles: occurrence records of sequenced specimens included in this study. The grids indicate those used in the previous global richness prediction analysis (see Lücking et al. 2014).

cloud forests ranging from the Sierra Madre Oriental through the central volcanic belt to the Sierra Madre del Sur, Cora also extends far into the (north-)western coniferous forests of the Sierra Madre Occidental. The sequenced material from Veracruz and Oaxaca represents invariably endemic lineages that are here interpreted as 11 species and one subspecies (see taxonomic treatment below). Given the pronounced depression east of the Sierra Madre del Sur along the Isthmus of Tehuantepec, between Oaxaca and Chiapas, it is likely that these species will remain Mexican endemics, even with further sampling eastwards into Chiapas and Guatemala. We also expect that the material previously recorded from central and (north-)western Mexico represents additional, unrecognized species, mostly different from those now recognized for southeastern Mexico, given the underlying topography, with separation between the Sierra Madre Occidental, Oriental, and del Sur. Unfortunately, simple revision of the previously reported collections is not sufficient to clarify this, as fresh material is required to assess field characters and substrate ecology and to generate sequence data for accurate placement of these taxa.

In the study by Lücking et al. (2014), who predicted global species richness in the genus *Cora* using a quantitative, linear extrapolation technique based on a 370 \times 300–370 km² grid map (Fig. 3), Mexico was represented by 22 grids, with a single sequenced specimen from Jalisco (grid 20). Grid-based species richness was estimated at 2–3 species per grid in the Sierra Madre Occidental (grids 02, 07, 08, 12), up to eight species per grid in the Sierra Madre Oriental (grids 04, 09, 10, 14),

(2–)11–17 species per grid for the central volcanic belt and the Sierra Madre del Sur (grids 20-23, 30-31), and 36 per grid for the Sierra Madre de Chiapas extending far into Guatemala (grid 32). The 12 taxa based on the sequenced material correspond to grids 20, 22 and 23, for which two, 17 and five species were predicted, respectively. Our findings documented one, two and ten taxa for the three grids, respectively, with one (C. dewisanti subsp. mexicana) overlapping between grids 20 and 23. Notably, there was no overlap between the two taxa found in grid 22 (Veracruz) and the ten taxa in grid 23 (Oaxaca). The predicted grid total for the Mexican grids, excluding grid 36 with overlaps with Guatemala, was 80. Given the estimated mean grid predicted range of 2.66 for Cora species across the Americas (Lücking et al. 2014), this would result in 80/2.66 = 30 predicted species for Mexico excluding Chiapas. This number appears reasonable, considering that the thus-far sequenced material chiefly covers southeastern Mexico west of Chiapas, whereas, with the exception of a single specimen from Jalisco, the majority of the documented range for the genus in Mexico, specifically central Mexico and the entire Sierra Madre Occidental, has not yet been sampled for molecular analysis. We hypothesize that additional species unveiled in this vast area will largely be Mexican endemics. In contrast, the entirely undocumented but high predicted richness for Chiapas, likely adding another 30 species, will at least partly be shared with Guatemala. All together, we can thus expect about 60 species of Cora for Mexico, only 12 (20%) of which are now known. For comparison, thus far 108 species are recognized for the territory

of Colombia, which is little more than half the size of Mexico, 44 of which (40%) have been formally described (Lücking et al. 2013, 2017b).

The 12 sequenced taxa known so far from Mexico originated from 11 independent migration events, with the closest relatives identified from either Costa Rica or the northern Andes. This pattern is rather remarkable, given that most of these lineages were found growing in close geographic proximity, and suggests that multiple lineages of *Cora* migrated northwards from South America more or less simultaneously, at least on geological timescales. This is supported by the terminal position of all Mexican lineages and the observation that in a third of these lineages a Costa Rican species is the closest relative (Fig. S1).

Taxonomy

Cora benitoana Moncada, R.-E. Pérez & Lücking, sp. nov. (Fig. 4A–D)

MycoBank MB 832769

Diagnosis: A (medium-sized to) large *Cora* growing epiphytically on tree trunks over bryophytes, fresh with dark greygreen, distinctly narrowly undulate lobes lacking color zonation, with a glabrous surface and with distinct, whitish, glabrous to thinly pilose margins; hymenophore cyphelloid, in part forming strongly protruding dorsiventral basidiocarps with setose upper surface; differing from the closely related *C. barbulata* (known from Costa Rica) in the glabrous lobe surface, strongly projecting basidiocarps, and forest habitat.

Type: Mexico: Oaxaca. Santiago Comaltepec, Cerro Pelón; 17°34'40.2"N; 96°30'21.6"W; 2990 m; cloud forest (bosque mesófilo), 17 May 2015, B. Moncada & R.-E. Pérez-Pérez 10193 (EB-BUAP – holotype!; B – isotype!).

ITS barcoding sequence(s): KX772550 (isotype), KX772555, KX772557, KX772561, KX772567, KX772606 (paratypes).

Description. Thallus epiphytic on tree trunks, usually over mosses and liverworts (often Frullania), foliose, up to 20 cm across, composed of 10-30 semicircular, imbricate lobes; individual lobes 3-6 cm wide and 2-4 cm long, moderately to frequently branched and with short, radially branching sutures, surface dark grey-green when fresh, without concentric color zonation, with distinct, involute, light greyish margins, light bluish grey when dry and becoming light grey in the herbarium, without distinct concentric color zonation. Upper surface distinctly narrowly undulate and somewhat pitted when fresh, shallowly undulate to almost even when dry, glabrous; involute margins glabrous to thinly pilose; lower surface ecorticate, felty-arachnoid (representing the exposed medulla), whitish when fresh, becoming yellowish white in the herbarium. Thallus in section 150-200 µm thick, with upper cortex, photobiont layer and medulla; upper cortex diffusely viaduct-shaped, formed by a 20-30 µm thick layer of loosely packed, irregularly arranged to periclinal, 4-6 µm thick hyphae supported by a 30-50 µm high 'medullary' layer of spaced groups of anticlinal, 4–6 µm thick hyphae; photobiont layer 50–70 µm thick, aeruginous-green; medulla 30–50 µm thick, hydrophobic; clamp connections absent, papilliform hyphal appendages absent. Hymenophore cyphelloid, developed partly as irregular, resupinate patches mostly towards lobe margins, partly as shortly stipitate, strongly protruding basidiocarps beyond lobe margins, resupinate patches 10-30 mm long and 5-10 mm broad, with white (fresh) to cream-colored (in the herbarium), smooth surface and setose, involute margins, protruding basidiocarps distinctly cyphelloid, up to 10 mm long and broad, with setose upper surface; hymenophore in section 100–150 µm thick, resting on medullary layer or entirely protruding; hymenium composed of numerous palisade-like basidioles and basidia; basidioles $20-30 \times 5-6 \mu m$; basidia $30-40 \times 5-7 \mu m$, 4-sterigmate; basidiospores not observed. Chemistry: No substances detected by TLC.

Etymology. This new species is dedicated to Benito Pablo Juárez García, Mexican president from 1857 to 1872, of indigenous origin (Zapotec) from the state of Oaxaca. A progressive reformer, Benito Juárez is considered the 'Mexican Abraham Lincoln' and is the only individual whose birthday is a national holiday in Mexico.

Distribution and ecology. *Cora benitoana* is so far known from a small area in Oaxaca, growing epiphytically on tree trunks in cloud forest (bosque mesófilo) between 2000 and 3000 m.

Notes. This new species is well characterized by its unusually large, cyphelloid hymenophore developed mostly towards the lobe margins and partly as entirely protruding, shortly stipitate basidiocarps closely resembling those of the related, appressed-filamentous genus Cyphellostereum (Dal Forno et al. 2013). There are several other mid-sized to large epiphytic species with (dark) green color when fresh, but most feature a typically adnate, concentric-reticulate hymenophore over all of the lobe underside and most are smaller. Cora barbulata, described from Costa Rica (Ariyawansa et al. 2015), is most closely related and shares with C. benitoana the epiphytic growth habit and the cyphelloid hymenophore, as well as the absence of papilliform hyphal appendages on the lower medullary hyphae, but differs in the terminally more-branched lobes, the partially setose, more or less even lobe surface, the paramo habitat, and the ubication of the hymenophore on the lobe underside, without forming protruding basidiocarps. A similar cyphelloid hymenophore which also agrees in size and epiphytic habit is otherwise known from C. cyphellifera, known from Ecuador and Colombia (Lücking et al. 2013), but in that species the thallus is light aeruginous when fresh. The two species species are related but clearly set apart phylogenetically (see Fig. S1).

Additional specimens examined. MEXICO: Oaxaca. Santiago Comaltepec, Cerro Pelón; 17°34'40.2"N; 96°30'21.6"W; 2990 m; cloud forest (bosque mesófilo), 17 May 2015, B. Moncada & R.-E. Pérez-Pérez 10180, 10183, 10193, 10199, 10207 (EB-BUAP, B – paratypes!). Santiago Comaltepec, Cerro Las Antenas; 17°35'16.5"N; 96°27'2.7"W; 2190 m; cloud forest



Figure 4. Habit of new *Cora* taxa. A-D - C. *benitoana* (holotype and isotype), showing rewetted thallus with basidiocarps (A), close-up of basidiocarps on dry thallus in the field (B) and rewetted thallus (C), and lobe underside with marginal hymenophore (D). E, F - C. *buapana* (isotype), showing rewetted thallus (E), lobe underside with corticioid-concentrical hymenophore (F) and partly branched-coralloid papillae on lower medullary hyphae (insets).

(bosque mesófilo), 17 May 2015, B. Moncada & R.-E. Pérez-Pérez 10306 (EB-BUAP, B – paratypes!).

Cora buapana Moncada, R.-E. Pérez & Lücking, sp. nov. (Fig. 4E–F)

MycoBank MB 832770

Diagnosis: A medium-sized *Cora* growing epiphytically on branches of trees or shrubs over and between bryophytes, fresh with dark grey to olive-grey lobes lacking distinct color zonation, with a glabrous surface; hymenophore corticioid and distinctly concentrically arranged; differing from *C. lawreyana* in the elongate, finger-like, partly branched appendages on the

lower medullary hyphae, and from other similar-sized epiphytic species with hyphal appendages in the grey rather than green fresh color.

Type: Mexico: Oaxaca. Santiago Comaltepec, Cerro Las Antenas; 17°35'16.5"N; 96°27'2.7"W; 2190 m; cloud forest (bosque mesófilo), 17 May 2015, B. Moncada & R.-E. Pérez-Pérez 10305 (EB-BUAP – holotype!; B – isotype!).

ITS barcoding sequence(s): KX772554 (isotype), KX772571 (paratype).

Description. Thallus epiphytic on branches of trees and shrubs, usually over and between mosses and liverworts

(often Frullania), foliose, up to 15 cm across, composed of 5-25 semicircular, slightly imbricate lobes; individual lobes 1.5-3 cm wide and 1-2(-3) cm long, rather frequently branched at base, with thin radially branching sutures that often expose photobiont clusters to appear granulose-sorediate, surface dark grey to olive-grey when fresh, without concentric color zonation, with distinct, involute, light greyish margins, white-grey when dry and in the herbarium, without distinct concentric color zonation. Upper surface uneven when fresh and dry, glabrous; involute margins glabrous; lower surface ecorticate, felty-arachnoid (representing the exposed medulla), whitish when fresh, becoming yellowish white in the herbarium. Thallus in section 250-300 µm thick, with upper cortex, photobiont layer and medulla; upper cortex viaduct-shaped, formed by 20-30 µm thick layer of rather densely packed, \pm periclinal, 4–6 μ m thick hyphae supported by 50-80 µm high 'medullary' layer of spaced groups of anticlinal, 4-6 µm thick hyphae; photobiont layer 70–120 µm thick, aeruginous-green; medulla 30-70 µm thick, hydrophobic; clamp connections absent but lower medullary hyphae with scattered, papilliform to elongate-finger-like or flask-shaped, partly branched hyphal appendages 3-7 µm long and 2-3 µm thick. Hymenophore corticioid, forming resupinate, linear and partly branched and anastomosing patches across lobe underside in distinctly concentric arrangement, patches 3–15 mm long and 0.5–1 mm broad, with white (fresh) to cream- or flesh-colored (in the herbarium), smooth surface and glabrous to very minutely pilose, slightly involute margins; hymenophore in section 100-130 µm thick, resting on thick medullary layer; hymenium composed of numerous palisade-like basidioles and scattered basidia; basidioles $20-30 \times 5-6 \mu m$; basidia $30-35 \times 5-7 \mu m$, 4-sterigmate; basidiospores not observed. Chemistry: No substances detected by TLC.

Etymology. The epithet honors the Benemérita Universidad Autónoma de Puebla (BUAP), the oldest and largest university in the state of Puebla, founded in 1578 as a Jesuit college.

Distribution and ecology. *Cora buapana* has an ecology similar to that of *C. benitoana*, so far known from a small area in Oaxaca, growing epiphytically on tree trunks in cloud forest (bosque mesófilo) between 2000 and 3000 m. It is apparently rarer than the preceding species.

Notes. Cora buapana forms part of a rather large group of medium-sized, epiphytic, non-sorediate species described from Central America (Costa Rica), the northern and central Andes (Colombia, Ecuador, Bolivia) and the Galapagos (Dal Forno et al. 2017; Lücking et al. 2017b). Of these, *C. boleslia* (Bolivia), *C. haledana* (Costa Rica), *C. pastorum* (Colombia), *C. santacruzensis* (Galapagos) and *C. viliewoa* (Costa Rica) agree in the formation of papilliform appendages on the lower medullary hyphae and in the corticioid, concentrically arranged hymenophore (where known), but differ in the aeruginous to emerald- or olive-green fresh color of the

lobes. The sympatric *C. benitoana* (see above) can be readily distinguished by the dark grey-green, distinctly undulate lobes and the cyphelloid hymenophore forming strongly protruding basidiocarps, and anatomically by the absence of papilliform appendages on the lower medullary hyphae. The otherwise very similar but allopatric and only distantly related *C. lawreyana* differs chiefly in the short, mostly globose hyphal appendages in the lower medulla.

Additional specimens examined. MEXICO: Oaxaca. Santiago Comaltepec, Cerro Pelón; 17°34'40.2"N; 96°30'21.6"W; 2990 m; cloud forest (bosque mesófilo), 17 May 2015, B. Moncada & R.-E. Pérez-Pérez 10197 (EB-BUAP, B – paratypes!).

Cora dewisanti subsp. mexicana Moncada, R.-E. Pérez & Lücking, subsp. nov. (Fig. 5A–C)

MycoBank MB 832771

Diagnosis: A large to very large *Cora* growing terrestrially between bryophytes and other lichens, fresh with olive-grey lobes lacking distinct color zonation except when dry, with a glabrous surface and with distinct, whitish, glabrous to thinly pilose margins; hymenophore corticioid-cyphelloid, often protruding beyond the lobe margins; differing from subsp. *dewisanti* in the much larger thallus and lobes and in the hymenophore often protruding beyond the lobe margins, as well as the forest habitat ecology.

Type: Mexico: Oaxaca. Santiago Comaltepec, Cerro Pelón; 17°34'40.2"N; 96°30'21.6"W; 2990 m; cloud forest (bosque mesófilo), 17 May 2015, B. Moncada & R.-E. Pérez-Pérez 10196 (EB-BUAP – holotype!; B – isotype!).

ITS barcoding sequence(s): KX772549 (isotype), EU825957, KX772538, KX772543, KX772544, KX772545, KX772548, KX772552, KX772558, KX772559, KX772560, KX772562, KX772563, KX772569 (paratypes).

Description. Thallus terrestrial between mosses and liverworts (often Frullania) and other lichens (Hypotrachyna), foliose, up to 30 cm across, composed of 10-30 semicircular, imbricate lobes; individual lobes 3-8 cm wide and 2-6 cm long, moderately to frequently branched and with short, radially branching sutures, surface olive-grey when fresh, without concentric color zonation, with distinct, involute, whitish to greyish margins, light bluish grey when dry and becoming grey with yellowish margins in the herbarium, with distinct concentric color zonation of paler and darker areas. Upper surface even to shallowly undulate when fresh, undulate-rugose when dry, glabrous; involute margins glabrous to shortly pilose, characteristically enrolled when dry, forming triangular patterns across lobes; lower surface ecorticate, felty-arachnoid (representing the exposed medulla), whitish when fresh, becoming yellowish white in the herbarium. Thallus in section 300–400 µm thick, with upper cortex, photobiont layer and medulla; upper cortex diffusely viaduct-shaped, formed by 150-200 µm thick layer of loosely and irregularly arranged, 4–6 μm thick hyphae; photobiont layer 70-100 µm thick, orangebrown above, olive-green below; medulla 30-70 µm

thick, hydrophobic; clamp connections absent, papilliform hyphal appendages absent. Hymenophore corticidoid-cyphelloid, developed as rounded to elongate, resupinate patches, mostly towards lobe margins and often protruding beyond them, sometimes also extending over nearby bryophytes, patches 5–30 mm long and 2–5 mm broad, often irregularly aggregate, with white to cream-colored, smooth surface and felty, involute margins; hymenophore in section 100–150 µm thick, resting on thick medullary layer; hymenium composed of numerous palisade-like basidioles and basidia; basidioles $20-35 \times 5-7$ µm; basidia $30-35 \times 5-7$ µm, 4-sterigmate; basidiospores not observed. Chemistry: No substances detected by TLC.

Etymology. The subspecific epithet refers to the distinctive distribution of this lineage as a putative Mexican endemic.

Distribution and ecology. This is so far the most widely distributed taxon in Mexico, known from the states of Jalisco and Oaxaca, suggesting a distribution along the central volcanic belt. The nominal subspecies is also rather widely distributed in the northern Andes (Colombia, Venezuela, Ecuador; Lücking et al. 2017b), indicating increased dispersal capacity in this lineage as compared to most other species of *Cora* (Lücking et al. 2014). Whereas subsp. *dewisanti* grows in paramos above 3000 m in the northern Andes, subsp. *mexicana* has so far been found only in cloud forest (bosque mesófilo) between 2000 and 3000 m.

Notes. Cora dewisanti subsp. mexicana is phylogenetically nested within C. dewisanti, where it forms a monophyletic clade differing from the nominal subspecies consistently in four insertions in the ITS. While the nominal subspecies appears to be widespread in Colombia, Venezuela and Ecuador, subsp. mexicana has so far been found only in Mexico. Together with the nested position, this merits recognition at infraspecies level rather than as a distinct species. The taxonomic distinction is supported by the morphometric and ecological differences, with subsp. mexicana developing much larger thalli and lobes and a more robust hymenophore not protruding beyond the lobe margins, and growing in forest habitats, but otherwise agreeing in overall morphology.

Additional specimens examined. MEXICO: Jalisco. Parque Nacional Volcán Nevado de Colima, beyond entrance station in La Joya area near the campground; 19°35'N, 103°36'W, 3415 m; 26 December 2006, R. Egan 17538 (OMA). Oaxaca. Ixtlán de Juárez, Desviación a San Pedro de Yaneri; 17°24'29.9"N; 96°29'59"W; 2978 m; cloud forest (bosque mesófilo), 17 May 2015, B. Moncada & R.-E. Pérez-Pérez 10154, 10176, 10322 (EB-BUAP, B – paratypes!). Santiago Comaltepec, Cerro Las Antenas; 17°35'16.5"N; 96°27'2.7"W; 2190 m; cloud forest (bosque mesófilo), 17 May 2015, B. Moncada & R.-E. Pérez-Pérez 10278, 10297, 10300, 10301, 10302 (EB-BUAP, B – paratypes!). Santiago Comaltepec, Cerro Pelón; 17°34'40.2"N; 96°30'21.6"W; 2990 m; cloud forest (bosque mesófilo), 17 May 2015, B. Moncada & R.-E. Pérez-Pérez 10185, 10195, 10198, 10228 (EB-BUAP, B – paratypes!). Cora guzmaniana Moncada, R.-E. Pérez & Lücking, sp. nov. (Fig. 5D–F)

MycoBank MB 832772

Diagnosis: A medium-sized *Cora* growing epiphytically on tree trunks over bryophytes, fresh with dark grey lobes lacking distinct color zonation, with a mostly glabrous surface but with indistinct concentric lines of scattered setae, especially towards the margin, and with distinct, whitish, glabrous to thinly pilose margins; lower medullary hyphae with coralloid, often spinulose hyphal appendages; hymenophore corticioid, forming elongate, concentrically arranged patches; differing from *C. buapana* chiefly in the partly setose lobe surface and the larger, coralloid and spinulose hyphal appendages on the lower medullary hyphae.

Type: Mexico: Oaxaca. San Vicente, Nuñú, Teposcolola; 17°24'N; 97°26'W; 2616 m; conifer forest (bosque de *Juniperus*), 14 November 2017, R.-E. Pérez-Pérez & D. León-González 1327 (EB-BUAP – holotype!; B – isotype!).

ITS barcoding sequence(s): MN475939 (isotype), MN475936, MN475937, MN475938, MN475940, MN475941, MN475942, MN475943, MN475944, MN475945, MN475946, MN475947, MN475948, MN475949, MN475950, MN475951 (paratypes).

Description. Thallus epiphytic, on Juniperus flaccida between mosses and other lichens (Flavoparmelia, Leucodermia and Parmotrema), foliose, up to 10 cm across, composed of 5-10 semicircular, partly imbricate lobes; individual lobes 1-3(-4) cm wide and 1-2 cm long, moderately to frequently branched and with short, radially branching sutures, surface dark grey when fresh, without concentric color zonation but more olive-grey towards margin, with distinct, involute, olive-grey margins, becoming white to light grey in the herbarium, without distinct concentric color zonation. Upper surface (un-) even when fresh, shallowly undulate to almost even when dry, mostly glabrous but with thin concentric lines of short, erect, thin, white setae, especially towards margin; involute margins glabrous to thinly pilose; lower surface ecorticate, felty-arachnoid (representing the exposed medulla), whitish when fresh, becoming yellowish white in the herbarium. Thallus in section 300-400 µm thick, with upper cortex, photobiont layer, and medulla; upper cortex diffusely viaduct-shaped, formed by 100-200 µm thick layer of loosely packed, irregularly arranged, 4-6 µm thick hyphae; photobiont layer 100-150 µm thick, olivegreen above, aeruginous-green below, sometimes above and below the photobiont layer with a 20-30 µm thick, orange-brown-pigmented layer of irregularly arranged hyphae; medulla 30-50 µm thick, hydrophobic; clamp connections absent but lower medullary hyphae with numerous shortly coralloid hyphal appendages 5-15 µm long and 5–10 µm thick, appearing somewhat spinulose due to short, thin hyphal outgrowths 2-3 µm long and 1-2 µm broad. Hymenophore corticioid, forming concentrically arranged, resupinate, rounded to elongate and sometimes branched patches across lower lobe surface, patches 1-5 mm long and 0.5-1 mm broad, with white (fresh) to cream-colored (in the herbarium), smooth surface and glabrous to minutely pilose, involute margins;



Figure 5. Habit of new *Cora* taxa. A-C - C. *dewisanti* subsp. *mexicana* (Moncada & Pérez-Pérez 10300), showing dry thallus in the field (A) and rewetted lobes (B) with partially protruding hymenophore, and lobe underside with marginal hymenophore (C). D-F - C. *guzmaniana* (D Pérez-Pérez & León-González 1334, E–F isotype), showing dry thallus with concentric rows of setae towards the lobe margins (D), rewetted thallus (E) and lobe underside with corticioid-concentric hymenophore (F).

hymenophore in section 70–100 μ m thick, resting on a multilayered medullary layer including older hymenial layers; hymenium composed of numerous palisade-like basidioles and basidia; basidioles 20–30 × 5–7 μ m; basidia 30–35 × 5–7 μ m, 4-sterigmate; basidiospores not observed. Chemistry: No substances detected by TLC.

Etymology. The epithet of this new species honors Gastón Guzmán Huerta [1932–2016], the most prominent Mexican mycologist, and colleague and mentor of the second author, for his paramount contributions to mycology in Mexico and Latin America as a whole

(Guzmán-Dávalos 2016; Mata & Salmones 2016; Guzmán-Dávalos & Cifuentes 2018).

Distribution and ecology. This new species is thus far known from only a single locality in Oaxaca, growing rather abundantly in patches of *Juniperus* trees immersed in upper montane conifer forest.

Notes. Cora guzmaniana is another medium-sized epiphytic species rather similar to *C. buapana*, including in the fresh color, but differs from the latter in the partly setose lobe surface, especially towards the margins, and in the peculiar, coralloid and often appearing spinulose hyphal appendages on the lower medullary hyphae. The only other medium-sized epiphytic species with a partly setose lobe surface and lower medullary hyphal papillae is *C. garagoa* from Colombia (Lücking et al. 2017b), which differs in the emerald-green, broadly undulate lobes, the adnate-confluent hymenophore, and the small, largely unbranched papilliform appendages on the lower medullary hyphae.

Additional specimens examined. MEXICO: Oaxaca. San Vicente, Nuñú, Teposcolola; 17°24'N; 97°26'W; 2616 m; conifer forest (bosque de *Juniperus*), 14 November 2017, R.-E.

Pérez-Pérez & D. León-González 1298, 1323, 1325, 1326, 1328, 1329, 1330, 1331, 1332, 1333, 1334, 1335, 1336, 1337, 1338 (EB-BUAP, B – paratypes!).

Cora ixtlanensis Moncada, R.-E. Pérez & Lücking, sp. nov. (Fig. 6A–C)

MycoBank MB 832773

Diagnosis: A medium-sized *Cora* growing terrestrially between bryophytes and other lichens, fresh with dark grey to olive-grey lobes lacking distinct color zonation except for a darker, marginal zone exposing the photobiont (best visible when drying), with a glabrous surface and lacking papilliform appendages on



Figure 6. Habit of new *Cora* taxa. A-C - C. *ixtlanensis* (holo- and isotype), showing dry thallus in the field (A), rewetted lobes (B), and lobe underside with corticioid-concentrical hymenophore (C). D-F - C. *lawreyana* (holo- and isotype), showing dry thallus in the field (D), rewetted lobes (E), lobe underside with corticioid-concentrical hymenophore (F) and globose papillae on lower medullary hyphae (insets).

the lower medullary hyphae; hymenophore corticioid, forming resupinate, elongate, concentrically arranged patches; similar to *C. terrestris* and differing from the latter only in molecular characters.

Type: Mexico: Oaxaca. Santiago Comaltepec, Cerro Pelón; 17°34'40.2"N; 96°30'21.6"W; 2990 m; cloud forest (bosque mesófilo), 17 May 2015, B. Moncada & R.-E. Pérez-Pérez 10205 (EB-BUAP – holotype!; B – isotype!).

ITS barcoding sequence(s): KX772547 (isotype), KX772539, KX772565 (paratypes).

Description. Thallus terrestrial between bryophytes (Breutelia, Thuidium) and other lichens (Cladonia), foliose, up to 15 cm across, composed of 10-20 semicircular, adjacent to slightly imbricate lobes; individual lobes 1.5-3 cm wide and 1-2.5 cm long, rather frequently branched at base, with short radially branching sutures, surface dark grey to olive-grey when fresh, without concentric color zonation, with distinct, involute, light greyish margins, light grey when dry and in the herbarium, without distinct concentric color zonation except for a darker marginal zone exposing the photobiont layer. Upper surface uneven to shallowly undulate when fresh and dry, glabrous; involute margins glabrous; lower surface ecorticate, felty-arachnoid (representing the exposed medulla), whitish when fresh, becoming yellowish white in the herbarium. Thallus in section 250–350 µm thick, with upper cortex, photobiont layer and medulla; upper cortex viaduct-shaped, formed by 20-30 µm thick layer of rather densely packed, periclinal, 4-6 µm thick hyphae supported by 50-80 µm high 'medullary' layer of spaced groups of anticlinal to oblique, 4–6 µm thick hyphae; photobiont layer 100-200 µm thick, olive-green above, aeruginous-green below; medulla 30-70 µm thick, hydrophobic; clamp connections absent, papilliform hyphal appendages absent. Hymenophore corticioid, forming resupinate, shortly elongate linear patches across lobe underside in distinctly concentric arrangement, patches 3-10(-20) mm long and 0.5-1 mm broad, with whitish (fresh) to cream- or flesh-colored (in the herbarium), smooth surface and glabrous to minutely pilose, slightly involute margins; hymenophore in section 100-150 µm thick, resting on thick medullary layer; hymenium composed of numerous palisade-like basidioles and scattered basidia; basidioles 20–30 \times 5–7 µm; basidia 25–35 \times 5–7 µm, 4-sterigmate; basidiospores not observed. Chemistry: No substances detected by TLC.

Etymology. We dedicate this new species to the Ixtlán community of the town of Ixtlán de Juárez in the state of Oaxaca, renowned for their sustainable ecosystem management and ecotourism (Bray 2016; Vázquez-Maguirre 2018; Pazos-Almada & Bray 2018).

Distribution and ecology. This new species is thus far known from only a single location, growing terrestrially in an upper montane cloud forest (bosque mesófilo) which is thus far the location richest in documented *Cora* lineages, with six species and one subspecies, including the also terrestrial *C. casasolana* and *C. dewisanti* subsp. *mexicana*.

Notes. Cora ixtlanensis is closely related and very similar to C. terrestris described from Costa Rica (Lücking et al. 2017b). Both are terrestrial and form medium-sized thalli and lobes with olive-grey color when fresh. They also share the corticioid hymenophore with resupinate, elongate patches in a concentric arrangement, and both lack papilliform appendages on the lower medullary hyphae. Since the two lineages are phylogenetically distinct, differing consistently in five positions in the ITS, we consider this to be one of the few examples of cryptic speciation known so far within the genus. Other medium-sized terrestrial species with more or less grey fresh color are C. celestinoa described from Colombian paramos and C. palustris known from montane forest in Costa Rica, which agree in the type of hymenophore and the absence of papilliform appendages on the lower medullary hyphae and hence can also be considered cryptic, although their upper cortex appears more dense and not distinctly viaduct-shaped (Lücking et al. 2017b). Notably, the two are not related to each other or to C. ixtlanensis and C. terrestris. Cora ixtlanensis grows sympatrically with C. casasolana and C. dewisanti subsp. mexicana; the first differs in the olive-green fresh color and the papilliform appendages on the lower medullary hyphae, whereas the second forms much larger thalli and lobes, with the hymenophore becoming partly cyphelloid and developed mainly towards the lobe margins.

Additional specimens examined. MEXICO: Oaxaca. Santiago Comaltepec, Cerro Pelón; 17°34'40.2"N; 96°30'21.6"W; 2990 m; cloud forest (bosque mesófilo), 17 May 2015, B. Moncada & R.-E. Pérez-Pérez 10264, 10293 (EB-BUAP, B – paratypes!).

Cora lawreyana Moncada, R.-E. Pérez & Lücking, sp. nov. (Fig. 6D–F)

MycoBank MB 832774

Diagnosis: A medium-sized (to large) *Cora* growing epiphytically on tree trunks over bryophytes, fresh with aeruginous-grey to marginally olive-green lobes lacking distinct color zonation, with a glabrous surface and with distinct, whitish, glabrous to thinly pilose margins; hymenophore corticioid, forming resupinate, elongate, concentrically arranged patches; lower medullary hyphae with short, mostly subglobose appendages; differing from *C. buapana* chiefly in the thicker, subglobose hyphal appendages.

Type: Mexico: Veracruz. La Cortadura Ecological Reserve; 19°29'N; 97°2'W; 2088 m; cloud forest (bosque mesófilo), 21 March 2017, R.-E. Pérez-Pérez & G. Águila-Rodríguez 1168 (EB-BUAP – holotype!; B – isotype!).

ITS barcoding sequence: MN475935 (isotype).

Description. Thallus epiphytic on branches of *Baccharis*, between mosses and liverworts (*Frullania*) and other lichens (*Leucodermia*, *Parmotrema* and *Usnea*), foliose, up to 10 cm across, composed of 5–10 semicircular, partly imbricate lobes; individual lobes 1-3(-4) cm wide and 1-3 cm long, moderately to frequently branched and with distinct, radially branching sutures, surface dark aeruginous-grey to olive-green towards margins when fresh, without concentric color zonation, with distinct,

involute, light grey margins, becoming white to light grey in the herbarium, without distinct concentric color zonation. Upper surface uneven when fresh, ±even to rugose when dry, glabrous; involute margins glabrous to thinly pilose; lower surface ecorticate, felty-arachnoid (representing the exposed medulla), whitish when fresh, becoming yellowish white to bluish grey in the herbarium. Thallus in section 200-250 µm thick, with upper cortex, photobiont layer, and medulla; upper cortex viaduct-shaped, formed by 10-20 µm thick layer of loosely packed, periclinal, 4-6 µm thick hyphae supported by 30-50 µm high 'medullary' layer of spaced groups of irregularly arranged to anticlinal, 4-6 µm thick hyphae; photobiont layer 50-80 µm thick, aeruginous- to emerald-green; medulla 50–100 µm thick, hydrophobic; clamp connections absent but lower medullary hyphae with numerous papilliform, unbranched, mostly globose hyphal appendages 2-3(-5) µm long and 2-3 µm thick. Hymenophore corticioid, distinctly concentrically arranged, forming resupinate, elongate to linear, partly branched to anastomosing patches across lower lobe surface, patches 1-10 mm long and 0.5-1 mm broad, with white (fresh) to cream-colored (in the herbarium), smooth surface and glabrous to minutely pilose, involute margins; hymenophore in section 100-120 µm thick, resting on medullary layer or entirely protruding; hymenium composed of numerous palisade-like basidioles and basidia; basidioles $20-35 \times 5-7 \mu m$; basidia $30-40 \times 5-7 \mu m$, 4-sterigmate; basidiospores not observed. Chemistry: No substances detected by TLC.

Etymology. We are delighted to dedicate this new species to our colleague and friend James D. ('Jim') Lawrey on the occasion of his 70th birthday. Jim has made numerous contributions to lichenology in such diverse fields as ecology, lichenicolous fungi, and the evolution of basidiolichens and their photobionts.

Distribution and ecology. Known from only a single locality in cloud forest (bosque mesófilo) in the state of Veracruz.

Notes. *Cora lawreyana* is similar to the apparently allopatric *C. buapana* and differs from the latter and other similar species (discussed under *C. buapana*) chiefly in the mostly globose appendages on the lower medullary hyphae.

Cora marusae Moncada, R.-E. Pérez & Lücking, sp. nov. (Fig. 7A-B)

MycoBank MB 832775

Diagnosis: A small, epiphytic *Cora* with abundant, marginal and partly laminal soredia and marked color contrast between fresh and dry lobes: fresh lobes with dark forest-green color and lighter olive-brown to olive-grey soredia, and dry lobes with white-grey color and dark olive-grey soredia; lower medullary hyphae with papilliform appendages; differing from the morphologically cryptic but phylogenetically unrelated *C. comaltepeca* in the dark forest-green rather than olive-green lobes when fresh, and in the much more abundant soredia.

Type: Mexico: Oaxaca. Santiago Comaltepec, Cerro Las Antenas; 17°35'16.5"N; 96°27'2.7"W; 2190 m; cloud forest (bosque mesófilo), 17 May 2015, B. Moncada & R.-E. Pérez-Pérez 10316 (EB-BUAP – holotype!; B – isotype!).

ITS barcoding sequence(s): KX772564 (isotype), KX772541, KX772542, KX772553, KX772570 (para-types).

Description. Thallus epiphytic on tree trunks, often overgrowing mosses and liverworts (including Frullania, Metzgeria, Plagiochila), foliose, up to 3 cm across, composed of 5-10 semicircular, adjacent to subimbricate lobes; individual lobes 0.5-1(-1.5) cm wide and 0.5-0.7(-1) cm long, sparsely branched, without radially branching sutures, surface dark forest-green when fresh, without concentric color zonation, with distinct, involute margins covered by lighter olive-brown to olive-grey soredia, surface becoming white-grey and soredia becoming dark olive-grey in the herbarium. Upper surface uneven to shallowly narrowly undulate when fresh, undulate to rugose when dry, glabrous, with diffuse concentric bands of scattered to dense soredia; involute margins glabrous, densely sorediate; lower surface ecorticate, appressed felty-arachnoid (representing the exposed medulla) and with photobiont layer partially protruding, whitish when fresh, becoming light yellowish grey in the herbarium. Thallus in section 250-300 µm thick, with upper cortex, photobiont layer and medulla; upper cortex viaduct-shaped, formed by 20-30 µm thick layer of loosely packed, periclinal, 4-6 µm thick hyphae supported by 50-100 µm high 'medullary' layer of spaced groups of irregularly arranged to oblique, 4-6 µm thick hyphae; photobiont layer 80-150 µm thick, olive-green above, aeruginous-green below, soredia aeruginous-green; medulla 30-50 µm thick; clamp connections absent but lower medullary hyphae with numerous papilliform, mostly unbranched hyphal appendages 3-5 µm long and 1.5–3 µm thick. Hymenophore not observed. Chemistry: No substances detected by TLC.

Etymology. We dedicate this new species to our colleague, mentor and friend María de los Ángeles Herrera-Campos ('Marusa') for her important contributions to the development of modern lichenology in Mexico.

Distribution and ecology. Found sympatrically with *Cora benitoana* and *C. buapana* (see above) in Oaxaca, growing epiphytically on tree trunks in cloud forest (bosque mesófilo) between 2000 and 3000 m.

Notes. Cora marusae is morphologically and anatomically similar to three other small (to medium-sized) epiphytic species producing soredia but with a glabrous, undulating lobe surface and featuring papilliform appendages on the lower medullary hyphae. All three are olive-green rather than forest-green, although this difference may be difficult to discern. The hymenophore in the somewhat related *C. rothesiorum* known from Colombia is also unknown, but that species differs from *C. marusae* in habitat ecology, being found in paramo vegetation (Lücking et al. 2017b). In both *C. comaltepeca* (Mexico) and *C. soredavidia* (Costa Rica and Brazil) the hymenophore is known and is distinct in the two species: corticioid-concentric

in the first, and cyphelloid and disc-shaped in the second (Lücking et al. 2017b). Both are unrelated to *C. marusae* and *C. rothesiorum*. Thus, hymenophore type may provide a good diagnostic character in these otherwise highly similar species. *Cora minor* and *C. paraminor* are closely related to *C. marusae* and also feature small sorediate lobes, but the soredia are marginal and the two species lack hyphal appendages on the lower medullary hyphae. Within Mexico, *C. marusae* is a very characteristic and readily recognized species, due to the heavily sorediate margins and the formation of concentric bands

of soredia also on the lobe surface. The taxon most likely to be confused is the sympatric *C. comaltepeca* (Lücking et al. 2017b), which is, however, phylogenetically very distinctive; it usually produces only a few soredia but the available material so far is too sparse to assess this variation quantitatively. In both species the color contrast between fresh and dry thalli is also remarkable, with the soredia being lighter than the lobe surface in the hydrated stage and becoming much darker in the herbarium. *Cora totonacorum* (see below) is also similar but produces larger lobes; it is not closely related to *C. marusae*.



Figure 7. Habit of new *Cora* taxa. A, B - C. *marusae* (A isotype, B Moncada & Pérez-Pérez 10178), showing rewetted (A) and dry (B) lobes with largely marginal soredia. C, D - C. *totonacorum* (isotype), showing rewetted (C) and dry (D) lobes with largely marginal soredia; lobe in D with attack by unidentified fungus. E, F - C. *zapotecorum* (isotype), showing rewetted lobes with thin setae (E) and lobe underside with corticioid-concentrical, partly confluent hymenophore (F).

Additional specimens examined. MEXICO: Oaxaca. Santiago Comaltepec, Cerro Pelón; 17°34'40.2"N; 96°30'21.6"W; 2990 m; cloud forest (bosque mesófilo), 17 May 2015, B. Moncada & R.-E. Pérez-Pérez 10178, 10212, 10222, 10319 (EB-BUAP, B – paratypes!).

Cora totonacorum Moncada, R.-E. Pérez & Lücking, sp. nov. (Fig. 7C–D)

MycoBank MB 832776

Diagnosis: A medium-sized *Cora* growing epiphytically on tree trunks, fresh with olive-grey to olive-green lobes with some color zonation, with a glabrous surface and with marginal soredia; lower medullary hyphae with papilliform appendages; similar and related to the allopatric *C. davidia* but differing phylogenetically in a large number of substitutions and indels.

Type: Mexico: Veracruz. La Cortadura Ecological Reserve; 19°29'N; 97°2'W; 2088 m; cloud forest (bosque mesófilo), 21 March 2017, R.-E. Pérez-Pérez & G. Águila-Rodríguez 1189b (EB-BUAP – holotype!; B – isotype!).

ITS barcoding sequence: MN475934 (isotype).

Description. Thallus epiphytic on branches of *Bac*charis, between mosses and liverworts (Frullania) and others lichens (Leucodermia, Parmotrema and Usnea), foliose, up to 7 cm across, composed of 3-5 semicircular, adjacent to subimbricate lobes; individual lobes 1-3 cm wide and 1-2 cm long, ascending, sparsely to moderately branched, without distinct, radially branching sutures, surface dark olive-grey to olive-green when fresh (towards margins), with some concentric color zonation alternating with lighter grey zones, with thin, flat to involute margins covered by olive-green soredia, surface becoming white-grey and soredia becoming dark olive-grey in the herbarium. Upper surface even to very shallowly undulate when fresh, shallowly undulate to rugose when dry, glabrous or with scattered, thin, white setae towards margins; involute margins glabrous to minutely pilose; lower surface ecorticate, felty-arachnoid (representing the exposed medulla), whitish when fresh, becoming light grey in the herbarium. Thallus in section 250-300 µm thick, with upper cortex, photobiont layer and medulla; upper cortex distinctly viaduct-shaped, formed by 30-50 µm thick layer of rather densely packed, periclinal, 4-6 µm thick hyphae supported by 50-70 µm high 'medullary' layer of loosely arranged, ±anticlinal, 4–6 μm thick hyphae; photobiont layer 50–100 μm thick, olive-green above, aeruginous-green below; medulla 30–60 µm thick; clamp connections absent but lower medullary hyphae with numerous papilliform, mostly unbranched hyphal appendages 3–5 µm long and 2–3 µm thick. Hymenophore not observed. Chemistry: No substances detected by TLC.

Etymology. The epithet honors the indigenous Totonac people, who inhabit the states of Veracruz, Puebla and Hidalgo. Their language belongs to a small, isolated language family without any known relatives (Sandstrom & García-Valencia 2005; Mackay & Trechsel 2018). During the 19th century the Totonac were the most important producers of vanilla (Rain & Lubinsky 2011; Cameron 2012).

Distribution and ecology. Known from only a single locality in cloud forest (bosque mesófilo) in the state of Veracruz, growing sympatrically with *C. lawreyana*.

Notes. Thus far there are three other medium-sized epiphytic species known to produce soredia and to feature papilliform appendages on the lower medullary hyphae: *Cora davidia* (Colombia to Ecuador), *C. inversa* (Colombia) and the widespread *C. hawksworthiana* (Costa Rica to Chile). All three occur in paramo to puna vegetation or temperate grasslands, but agree with *C. totonacorum* in the more or less olive-green color. *Cora inversa* differs from the other three species in the rather large papilliform appendages on the lower medullary hyphae, whereas the remaining three taxa are more or less cryptic morphologically and anatomically. Whereas *C. hawksworthiana* and *C. inversa* are only distantly related, *C. davidia* is close to *C. totonacorum*, although the two differ phylogenetically in 13 substitutions and two indels in the ITS.

Cora zapotecorum Moncada, R.-E. Pérez & Lücking, sp. nov. (Fig. 7E–F)

MycoBank MB 832777

Diagnosis: A small (to medium-sized) *Cora* growing epiphytically on branches of trees or shrubs over and between bryophytes, fresh with olive-grey lobes lacking distinct color zonation, with a mostly glabrous surface and with concentric areas of appressed setae (erect when wet), and with distinct, whitish, glabrous to thinly pilose margins; hymenophore \pm cyphelloid, forming rounded to elongate patches; differing from *C. hoches-uordensis* and *C. schizophylloides* in the very thinly pilose lobe surface and the corticioid-concentrical hymenophore.

Type: Mexico: Oaxaca. Santiago Comaltepec, Cerro Pelón; 17°34'40.2"N; 96°30'21.6"W; 2990 m; cloud forest (bosque mesófilo), 17 May 2015, B. Moncada & R.-E. Pérez-Pérez 10206 (EB-BUAP – holotype!; B – isotype!).

ITS barcoding sequence(s): KX772568 (isotype), KX772546, KX772566 (paratypes).

Description. Thallus epiphytic on branches of trees and shrubs, usually over and between mosses and liverworts (often Frullania), foliose, up to 8 cm across, composed of 5-15 semicircular, distant to slightly imbricate lobes; individual lobes 0.5-1.5 cm wide and 0.5-1 cm long, frequently branched at margins to appear marginally crenate to lobate, without radially branching sutures, surface dark olive-grey when fresh, without concentric color zonation, with distinct, involute, light greyish margins, white-grey when dry and in the herbarium, without distinct concentric color zonation. Upper surface uneven when fresh and dry, mostly glabrous but with concentric areas of strongly appressed setae arranged radially, becoming erect when wet; involute margins glabrous to thinly pilose; lower surface ecorticate, felty-arachnoid (representing the exposed medulla), whitish when fresh, becoming yellowish white in the herbarium. Thallus in section 300-350 µm thick, with upper cortex, photobiont layer and medulla; upper cortex viaduct-shaped, formed by 20-30 µm thick layer of rather densely packed, irregularly arranged to periclinal, 4-6 µm thick hyphae supported by 50-100 µm high

'medullary' layer of spaced groups of anticlinal, 4–6 μm thick hyphae; photobiont layer 150-200 µm thick, olivegreen above, aeruginous-green below; medulla 30-70 µm thick, hydrophobic; clamp connections absent but lower medullary hyphae with scattered, papilliform, (sparsely) branched hyphal appendages 3-5 µm long and 2-4 µm thick. Hymenophore corticioid, forming resupinate, elongate to irregularly rounded patches across lobe underside, in more or less concentric arrangement and often closely adjacent to confluent, patches 2-5 mm long and 1-2 mm broad, with white (fresh) to cream-colored or flesh-colored (in the herbarium), smooth surface and glabrous, slightly involute margins; hymenophore in section 100-130 µm thick, resting on medullary layer; hymenium composed of numerous palisade-like basidioles and scattered basidia; basidioles 20–30 \times 5–7 µm; basidia 25–35 \times 5–7 µm, 4-sterigmate; basidiospores not observed. Chemistry: No substances detected by TLC.

Etymology. The epithet of this new species honors the Zapotec people, one of the most important indigenous civilizations in Mesoamerica, concentrated in the area today covered by the state of Oaxaca. The cultural history of the Zapotec goes back to 500 BCE and perhaps as far back as 1150 BCE, and lasted until the early 16th century (Marcus & Flannery 1996).

Distribution and ecology. Found sympatrically with *Cora benitoana*, *C. buapana* and *C. marusae* (see above) in Oaxaca, growing epiphytically on branches in cloud forest (bosque mesófilo) between 2000 and 3000 m.

Notes. Thus far, only two other small (to medium-sized) epiphytic species are known to produce setae on the lobe surface and feature papilliform appendages on the lower medullary hyphae: *C. hochesuordensis* from the Bolivian puna and *C. schizophylloides* from the Colombian paramo (Lücking et al. 2017b). Both differ in the more densely pilose-setose lobe surface and the distinctly cyphelloid hymenophore. Within Mexico, *C. zapotecorum* is most similar to the sympatric *C. marusae* but lacks soredia and differs in the partly pilose-setose lobe surface.

Additional specimens examined. MEXICO: Oaxaca. Santiago Comaltepec, Cerro Las Antenas; 17°35'16.5"N; 96°27'2.7"W; 2190 m; cloud forest (bosque mesófilo), 17 May 2015, B. Moncada & R.-E. Pérez-Pérez 10307 (EB-BUAP, B – paratypes!). Santiago Comaltepec, Cerro Pelón; 17°34'40.2"N; 96°30'21.6"W; 2990 m; cloud forest (bosque mesófilo), 17 May 2015, B. Moncada & R.-E. Pérez-Pérez 10318 (EB-BUAP, B – paratypes!).

Key to the species of *Cora* thus far known from southeastern Mexico

- 409

3(2) Soredia abundant and dense; hymenophore unknown C. marusae Soredia sparse; hymenophore usually present, corticioid, forming resupinate, elongate, concentrically arranged patches C. comaltepeca

- 8(7) Lower medullary hyphal appendages short, mostly globose..... C. lawreyana Lower medullary hyphal appendages elongate and finger-like or flask-shaped, partly branched... C. buapana

..... C. ixtlanensis

rarely up to 4 cm; lower medullary hyphae with or with-

11(10) Lobes aeruginous-green when fresh; growing in montane forest; upper cortex collapsed-compacted; hymenophore corticioid, forming elongate, concentrically arranged, resupinate patches.
Lobes olive-green (to olive-grey) when fresh; growing in subalpine vegetation; upper cortex viaduct-shaped; hymenophore unknown

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Supplementary electronic material

Figure S1. Complete, best-scoring phylogenetic ML tree of the ITS sequences of *Cora* used in this study. Supported branches are thickened and bootstrap support values are indicated above the branches. Samples from Mexico are highlighted in orange. Download file

 Table S1. Genbank accession numbers and geographic origin for the ITS sequences of *Cora* used in this study. Download file

Table S2. Georeference data for specimens of *Cora* reported from Mexico used to generate the map in Fig. 3, including specimens available through GBIF and CNALH and the specimens analysed (sequenced) in the present work. Download file

File S1. Complete alignment of the ITS sequences of *Cora* used in this study. Download file

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