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Lichens in Puerto Rico: An Ecosystem Approach

Joel A. Mercado-Díaz, William A. Gould, Grizelle González, and Robert Lücking

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Cover: *Herpothallon rubrocinctum* growing on a bamboo shoot (*Bambusa vulgaris*) in the Central Mountain Range, Puerto Rico. Photo by J.A. Mercado-Díaz.

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Abstract

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This work presents basic information on tropical lichenology. It also describes general aspects about the ecology and biodiversity of these organisms in eight forest ecosystems present along an elevational gradient in northeastern Puerto Rico. These ecosystems consist of elfin woodlands, palo colorado, sierra palm, tabonuco, lowland moist, dry, mangrove, and *Pterocarpus* forests. Lichen communities are mainly described in terms of general ecological attributes (e.g., species richness, common species, etc.). Basic information about the environment and vegetation found in these forests is also provided. The information presented is supplemented with field and microscopic photographs of species and their habitats.

Keywords: Tropical lichens, Puerto Rico, forests, conservation.

Contents

Preface

This report aims to introduce the reader to general concepts in lichenology with a particular emphasis in tropical lichens and the study of lichens in Puerto Rico. It also intends to describe in a broad manner the main characteristics of lichen communities present in different forest ecosystems of the island, and the environmental conditions in which they thrive. Although care was taken in following basic rules for responsible scientific investigation and writing, the information presented here is aimed to appeal to a more general audience. Moreover, this work presents ideas that may stimulate the formation of new research questions concerning the lichen flora of Puerto Rico, and consequently increase interest in and appreciation for the study of this amazing group of symbiotic organisms.

Introduction

What Are Lichens?

For centuries, lichens have been an intriguing group of organisms for scientists mostly because of the difficulties that botanists and taxonomists have faced in their classification (fig. 1). Today, the symbiotic nature of lichens is well understood. In 1982, the International Association of Lichenology described lichens as "an association between a fungus and a "photosynthetic partner," which results in a stable thallus with a specific structure." Most of the fungi that become lichenized belong to the division Ascomycota. Only 1 percent of lichens have a fungal component from the division Basidiomycota. The fungal partner in a lichenological association is better known as the **mycobiont**, which is also the source for the species name in lichens. The photosynthetic partner, or **photobiont**, is usually an alga within the classes Trebouxiophyceae and Ulvophyceae (Leliaert et al. 2012). Cyanobacteria, formerly called "bluegreen algae," also participate in lichenization. In some lichens, such as species in the genus *Stereocaulon*, both algae and cyanobacteria may be found within the same thallus.

Lichens are a symbiotic association between a fungus and a photosynthethic partner.

Prompted by the symbiotic nature of lichens, scientists have been interested in studying how the mycobiont and the photobiont behave outside the lichen association. In fact, individual components of lichen species have been successfully separated in vitro; not surprisingly, their appearance is usually in sharp contrast to the lichenized form (fig. 2). The mycobiont is usually amorphous and has slow growth rates; therefore, it is believed that, for most of the mycobionts, lichenization is obligate (Nash 2008).

Depending on the species, the photobiont may grow successfully in a free-living state. For example, tropical filamentous algae *Trentepohlia* is commonly found free-living (fig. 3), but for the green algae *Trebouxia*, survival outside lichenization is rare.

Lichens come in a variety of colors and growth forms and are able to colonize almost every type of substrate that an environment could provide. Although the most common colors in lichens are grey, pale green, and yellowish-green, some species are capable of producing secondary compounds that make them orange, red, or yellow (Brodo et al. 2001). There are six main types of growth forms in lichens: **crustose**, **foliose**, **squamulose**, **fruticose**, **dimorphic**, and **pendulous** (fig. 4). The size of these growth forms is highly variable, from less than a few millimeters in some crustose species to more than 2 m in some pendulous *Usnea* species. Although the majority of species fit into one of these types, it is not uncommon to find intermediate forms.

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[1] Note: terms in boldfaced type are defined in the glossary (page 75).

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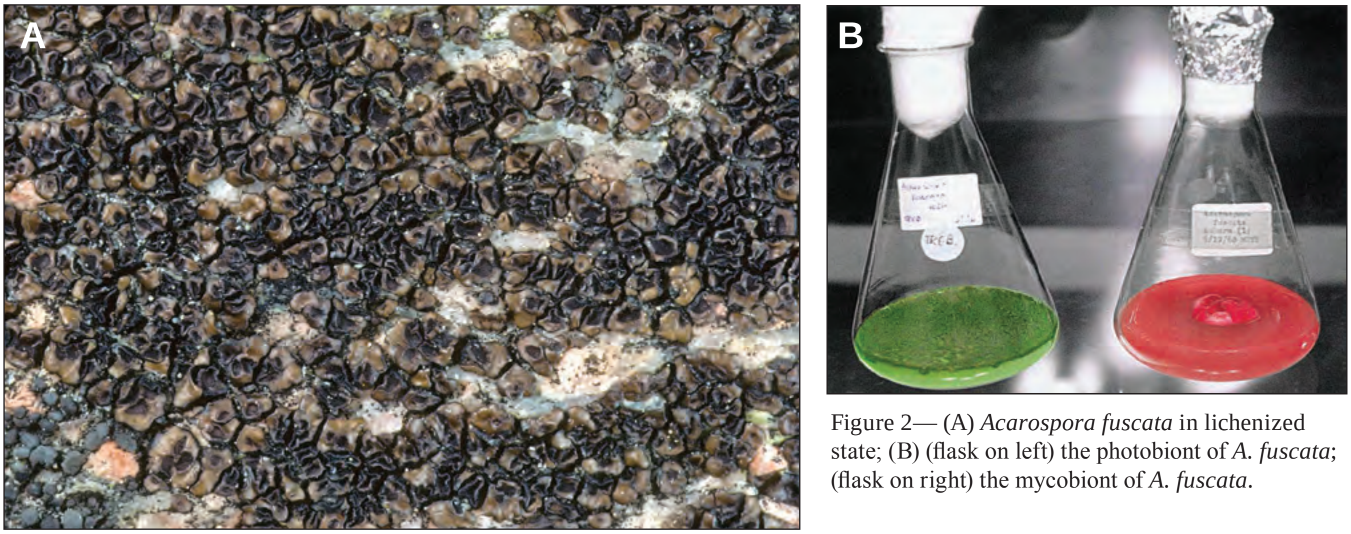
Figure 1—Lichens growing on a tree stump in Aibonito, Puerto Rico.



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Vernon Ahmadjian

Figure 2— (A) *Acarospora fuscata* in lichenized state; (B) (flask on left) the photobiont of *A. fuscata*; (flask on right) the mycobiont of *A. fuscata*.

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Figure 3—Colonies of *Trentepohlia* algae colonizing the branches of a tree in an elfin woodland forest, El Yunque National Forest, Puerto Rico.

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A. Cuevas-Padró
R. Lücking
A. Cuevas-Padró

Figure 4—Common growth forms found in lichens. (A) Crustose [*Graphis* spp.], El Yunque National Forest, Puerto Rico; (B) Foliose [*Sticta* spp.], El Yunque National Forest, Puerto Rico; (C) Squamulose [*Acarospora socialis*], Sierra Bermeja, Puerto Rico; (D) Fruticose [*Cladina sandstede*], Maricao, Puerto Rico; (E) Dimorphic [*Cladonia subradiata*], El Yunque National Forest, Puerto Rico; (F) Pendulous [*Usnea* spp.] Maricao, Puerto Rico. Photos by: J.A. Mercado-Díaz, R. Lücking, and A. Cuevas-Padró.

Rocks and the bark of trees are usually the preferred colonization substrates for lichens; however, they have been found growing on all types of natural and artificial substrates including leaves, wood, concrete, glass, plastic, and metal (fig. 5) or even the carapace of some insects (Lücking et al. 2010). Lichens produce a number of morphological and anatomical characteristics that their component organisms would not develop in their free-living forms (Ahmadjian 1993, Brodo et al. 2001, Nash 2008). Examples of these features include **cilia**, **rhizines**, and **cyphellae**. These attributes are also used for taxonomic identification.

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Figure 5—Several foliose and crustose lichens growing on human-made structures, Jardín Botánico Norte, Río Piedras, Puerto Rico.

In terms of nutrition, the photobiont provides most of the organic nutrients to the mycobiont. For green algal lichens, carbohydrates are transferred to the mycobiont in the form of sugar alcohols, and for cyanobacterial lichens in the form of glucose (Nash 2008, Purvis 2000). Benefits gained for the photobiont from lichenization are not so apparently obvious, especially because it has been observed that, in a lichenized state, some photobionts grow more slowly than in their free-living form (Nash 2008). In spite of this, studies have found that the mycobiont facilitates the absorption of mineral nutrients, enhances water uptake to the photobiont, and protects it from light damage in sun-exposed environments, which suggests that the photobiont does actually gain some benefits from lichenization.

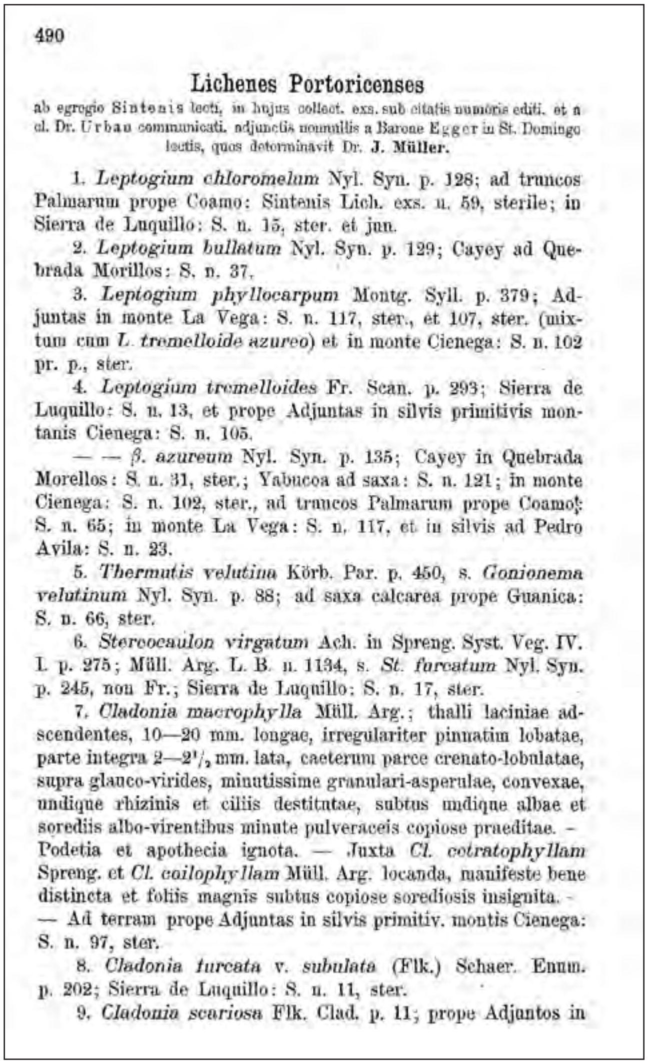
It remains undisputed that in the lichenized state, both the mycobiont and the photobiont are capable of thriving in environments in which they would not survive individually. This would probably explain why lichens colonize almost every ecosystem in the world, from tropical rain forests to polar environments (Brodo et al. 2001, Purvis 2000). In this respect, lichens were initially believed to be more diverse in temperate ecosystems, a notion supported by several misleading lichen surveys (Lücking et al. 2011). However, at smaller scales, (e.g., looking at uniform area sizes of 100 km^2, 10 km^2, 1 km^2, or even 1 ha), lichen species richness clearly increases toward lower latitudes (Lücking et al. 2011). Estimates of world species richness of lichens range from 13,500 (Hawksworth and Hill 1984) to 18,000 species (Sipman and Aptroot 2001). Yet, a more recent study has suggested that the extent of world species richness may be about 28,000, with at least half of the species (14,000) occurring in the tropics (Lücking et al. 2009a). Compared to their fungal counterpart, photobiont diversity is less conspicuous, with nearly 54 genera and about 100 species of algae and cyanobacteria reported (Ahmadjian 1967, Büdel 1992, Frey 2012, Tschermak-Woess 1988). For years lichenologists believed that lichen photobionts had little influence on thallus morphology. Nevertheless, recent discoveries, like the continually increasing description of new species forming **photosymbiodemes** (Moncada et al. 2013), shows that at least for some groups, photobionts have a stronger influence on thallus morphology than was previously supposed.

Because of the diversity of microorganisms that have been found to inhabit the lichen thallus, lichens are often regarded as "miniature ecosystems."

The symbiotic association of lichens is still a controversial topic among lichenologists and taxonomists, mostly because the nature of this association does not fit precisely in any of the known examples of ecological symbiosis. Perhaps the most appropriate categorization of the lichen symbiosis would be "controlled parasitism," because the mycobiont negatively affects the physiognomy and metabolism of the photobiont without killing it (Ahmadjian 1993, Schwendener 1869). Goward (1994) referred to this relationship as "fungi that have discovered agriculture." Evidence from a recently described lineage of cyanobacteria (Rhizonema) strongly supports this view of the lichen symbiosis (Lücking et al. 2009b). However, recent discoveries have shown that lichens are made of much more than fungal and photobiont components. A number of endolichenic bacteria and fungi with distinctive chemical properties have been found in different lichen thalli (Arnold 2007, Cardinale et al. 2006); hence lichens may be more appropriately regarded as miniature ecosystems (Nash 2008).

Lichenology in Puerto Rico

The field of lichenology in Puerto Rico began in 1820 with the identification of two species from Puerto Rico in a report by Sprengel (1820), and a subsequent report titled “Lichenes Portoricenses,” published by Jean Müller Argoviensis in 1888 (fig. 6). However, not until the beginning of the 20th century were significant contributions to Puerto Rican lichenology made by scientists from the United States and Europe. Some of these included world-renowned lichenologists of that era, such as Bruce Fink, Edvard A. Vainio, and Alexander Zahlbruckner (Mercado-Díaz and Santiago-Valentín 2010). Lichenology on the island was nearly abandoned until 1972 when a monograph of the lichen genus *Ramalina* in Puerto Rico and the Caribbean was presented by Landrón-Concepción (1972), then in the late 1980s with the publication of *Working Keys of Lichenized Fungi from Puerto Rico* (Harris 1989).



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Lichenes Portoricenses

ab egregio Sintenis lecti, in hujus collect. exs. sub citatis numeris editi, et a cl. Dr. Urban communicati, adjunctis nonnullis a Barone Egger in St. Domingo lectis, quos determinavit Dr. **J. Müller.**

1. *Leptogium chloromelum* Nyl. Syn. p. 128; ad truncos Palmarum prope Coamo: Sintenis Lich. exs. n. 59, sterile; in Sierra de Luquillo: S. n. 15, ster. et juv.

2. *Leptogium bullatum* Nyl. Syn. p. 129; Cayey ad Quebrada Morillos: S. n. 37.

3. *Leptogium phyllocarpum* Montg. Syll. p. 379; Adjuntas in monte La Vega: S. n. 117, ster., et 107, ster. (mixtum cum *L. tremelloide azureo*) et in monte Cienega: S. n. 102 pr. p., ster.

4. *Leptogium tremelloides* Fr. Scan. p. 293; Sierra de Luquillo: S. n. 13, et prope Adjuntas in silvis primitivis montanis Cienega: S. n. 105.

— — *β. azureum* Nyl. Syn. p. 135; Cayey in Quebrada Morellos: S. n. 31, ster.; Yabucoa ad saxa: S. n. 121; in monte Cienega: S. n. 102, ster., ad truncos Palmarum prope Coamo: S. n. 65; in monte La Vega: S. n. 117, et in silvis ad Pedro Avila: S. n. 23.

5. *Thermutis velutina* Körb. Par. p. 450, s. *Gonionema velutinum* Nyl. Syn. p. 88; ad saxa calcarea prope Guanica: S. n. 66, ster.

6. *Stereocaulon virgatum* Ach. in Spreng. Syst. Veg. IV. I. p. 275; Müll. Arg. L. B. n. 1134, s. *St. furcatum* Nyl. Syn. p. 245, non Fr.; Sierra de Luquillo: S. n. 17, ster.

7. *Cladonia macrophylla* Müll. Arg.; thalli laciniae adscendentes, 10—20 mm. longae, irregulariter pinnatim lobatae, parte integra 2—2½ mm. lata, caeterum parce crenato-lobulatae, supra glauco-virides, minutissime granulari-asperulae, convexae, undique rhizinis et ciliis destitutae, subtus undique albae et sorediis albo-virentibus minute pulveraceis copiose praeditae. — Podetia et apothecia ignota. — Juxta *Cl. cetratophyllam* Spreng. et *Cl. coilophyllam* Müll. Arg. locanda, manifeste bene distincta et foliis magnis subtus copiose sorediosis insignita. — — Ad terram prope Adjuntas in silvis primitiv. montis Cienega: S. n. 97, ster.

8. *Cladonia furcata* v. *subulata* (Flk.) Schaer. Enum. p. 202; Sierra de Luquillo: S. n. 11, ster.

9. *Cladonia scariosa* Flk. Clad. p. 11; prope Adjuntos in

Figure 6—Cover of the report *Lichenes Portorricenses*, published by Jean Müller Argoviensis in 1888.

Recent efforts promoting lichenology in Puerto Rico include the research project under which this report is supported: “Characterizing lichen communities along an elevational gradient in Puerto Rico: assessing their role as indicators of forest health, biodiversity and microclimate,” led by Joel A. Mercado-Díaz and William Gould. Also, a workshop titled “Taller de Liquenología Tropical: los micro y macro-líquenes de Puerto Rico,” held in 2011 at the University of Puerto Rico and organized by Joel A. Mercado-Díaz and Robert Lücking, resulted in the identification of at least 5 new lichen species and documentation of 25 species previously unknown to Puerto Rico, as well as the training of 14 participants in tropical lichenology (Mercado-Díaz 2011).

Finally, Lichens of Puerto Rico, a website at http://lichensofpuertorico.herbario.upr.edu/, presents a list of the currently known lichens and lichenicolous fungi species that occur in Puerto Rico (Mercado-Díaz 2009). For more information about the history of lichenology in Puerto Rico, refer to Mercado-Díaz and Santiago-Valentín (2010).

Lichens in Puerto Rican Ecosystems

By colonizing and accelerating the erosion of newly exposed surfaces, lichens facilitate the formation of soils.

Only occasionally do lichens comprise most of the biomass in forests; however, they play many ecological roles in these ecosystems (Will-Wolf et al. 2002). Lichens occupy nearly 8 percent of the Earth's terrestrial surface (Ahmadjian 1993), and it is highly likely that their most prominent role in terrestrial ecosystems is related to their ability to facilitate primary succession. In this respect, lichens are among the first organisms to colonize newly exposed surfaces, such as rocks formed after the cooling of recently erupted lava or soil exposed by a landslide. Lichen growth and expansion result in mechanical and chemical abrasion that speeds up the natural weathering process of these surfaces and therefore accelerates soil formation. Colonization over smooth, inhospitable rock surfaces is therefore the most important contribution lichens make to soil formation and consequently to primary colonization (Brodo et al. 2001).

Lichens are also important agents of soil stabilization and may represent a source of nitrogen and organic matter in some soils (Brodo et al. 2001, Jones 1988). Lichen colonization in disturbed and sandy soils may also be important for controlling erosion and the sedimentation of water bodies. As early colonizers, lichens are critical components of landslide recovery (Walker and Shiels 2013). In Puerto Rico, the growth of *Stereocaulon ramulosum* in recently exposed soil resulting from landslides or the construction and expansion of roads in mountainous areas of the island may constitute an important biological buffer against this type of disturbance (fig. 7a). Vast patches of different *Cladonia* species, like *C. subradiata* and the endemic *C. robusta*, have been observed growing in the siliceous sands of Laguna Tortuguero in Vega Baja and may contribute to reducing losses of sand via wind or water movement (fig. 7b).

As in other tropical regions, most of the lichen species in forests in Puerto Rico are **epiphytic**, classified either as **foliicolous** or **corticolous**. In areas of high


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R. Seavey and J. Seavey

Figure 7—(A) *Stereocaulon ramulosum* growing in recently exposed soil along a road in El Yunque National Forest, Puerto Rico; (B) Growth habit of *Cladonia subradiata*.

humidity with adequate light exposure (e.g., elfin woodlands in El Yunque National Forest), mosses and liverworts grow faster than lichens and therefore colonize most of the available epiphytic substrate area in these ecosystems. On the contrary, in forests with lower humidity like the Northern Karst Belt and the Guánica State Forest, lichens are possibly among the dominant epiphytes, at least in terms of the number of species.

Lichens are believed to have an important role in water and nutrient cycles in forest ecosystems (Beckett 1995, Green and Lange 1991, Zotz et al. 1998). For many species, the lichen thallus is capable of storing up to 800 percent of its dry weight in water. This water, which is initially absorbed by direct assimilation from water vapor or rainwater, is released slowly to the environment, thereby influencing the immediate microclimate. Tree-dwelling lichens absorb a significant amount of nutrients from rainwater that passes through the canopy over the leaves, and differentially absorb minerals as water flows down to the soil (Brodo et al. 2001, Knops et al. 1991). Fruticose lichens like *Ramalina menziesii* have been shown to significantly affect the interception of rainwater and the deposition of water and nutrients in throughfall collected beneath the canopy in some temperate ecosystems (Knops et al. 1996). These effects potentially influence the composition and concentration of nutrients in underlying soils. Although it is likely for this kind of influence on water and nutrient status in trees and soils to be considerable in some forest areas of Puerto Rico (especially those where fruticose and foliose lichens are frequent), little is known about this subject in tropical ecosystems, thus it represents a promising research topic that deserves further investigation.

It is possible that some of the nitrogen fixed by cyanobacterial lichens leaches from the lichen thallus or becomes available to neighboring plants when the lichen dies (Brodo et al. 2001), hence contributing to soil fertilization and consequently vegetation growth. Although quantitative estimates for this type of fertilization are scarce, it is not unreasonable to suggest that areas with the highest diversity and abundance of cyanobacterial lichens are the places where this mode of fertilization is more likely. One of the places in Puerto Rico where this may happen is in El Yunque National Forest, which has a relatively high diversity of species with cyanobacterial photobionts such as *Stereocaulon*, *Peltigera*, *Dictyonema*, and *Sticta*.

Some evidence appears to indicate that lichens are being used as a food source by several animals and insects in Puerto Rico. For instance, the tracks of what appears to be a snail possibly feeding on the thalli of several crustose species have been observed on numerous leaf, bark, and other artificial surfaces in El Yunque National Forest and other forests of the island[1] (fig. 8). Some of these tracks may

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[1] Mercado-Díaz, J.A. 2014. Personal observation.


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Figure 8—Lichen thallus with grazing “tracks” (reddish areas), which are evidence of the feeding activities of a snail. This lichen is growing on an artificial substrate (a car door).

belong to *Scharammia alta*, an endemic snail known from Luquillo and other places around the island that presumably feeds on encrusting algae and lichens.[2] Gastropod grazing and lichen growth have been negatively associated for years; however, recent studies suggest that gastropods grazing on lichens may represent important vectors for lichen dispersal (Bosh et al. 2011). On the other hand, the frequent observation of **pyrenocarpous** lichens lacking their fruiting bodies (perithecia) may represent important evidence of direct grazing by insects.

Lichens appear to be important nesting material for some bird species on the island. For example, fragments of foliose species like *Parmotrema* and *Hypotrachyna* are found in almost every hummingbird nest (fig. 9). These pieces of lichen are most likely part of a camouflage strategy by birds to evade predation of nestlings. Insects may also be using lichens for camouflage; there is documentation that the carapace of some tree-dwelling insects in Puerto Rico and Hispaniola resembles the patterns of lichens growing on leaves or tree trunks.[3] [4]

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[2] Robinson, D.G.; García-Díaz, W.; Fields, A.; Pérez, J., Tang, T. 2011. The terrestrial malacofauna of Puerto Rico and the U.S. Virgin Islands. Unpublished manuscript. Washington, DC: U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Plant Protection and Quarantine. 107 p.

[3] Mercado-Díaz, J.A. 2014. Personal observation.

[4] Torres-Santana, C. 2014. Personal observation. Director, Arboretum Parque Doña Inés, Fundación Luis Muñoz Marín, RR 2 Buzón #5, San Juan, PR 00926-9766.


José González Díaz

Figure 9—A hummingbird resting in a nest completely covered with foliose lichens.

There may be around 2,000 species of lichens in Puerto Rico, which represents nearly half of the species known for the continent of North America.

There are at least 1,181 recognized species of lichenized fungi in Puerto Rico (Mercado-Díaz 2009); however, a recently published work proposes that the island may harbor around 1,600 species (Lücking et al. 2009a). Based on the checklist of lichens and lichenicolous fungi of Puerto Rico (Mercado-Díaz 2009) and preliminary results from a tropical lichenology workshop in the island (Mercado-Díaz 2011), the real diversity of the island may reach about 2,000 species. This is almost half of the species known for the whole continent of North America.[5]

Methods

Study Areas

Most of the information presented in this report comes from intensive lichen collecting activities conducted by Joel A. Mercado-Díaz between August 2011 and October 2012. Lichens were collected around the periphery of 10 × 10 m^2 plots that were established for a study characterizing several biological and environmental parameters along an elevational gradient (fig. 10; González and Luce 2013; González et al. 2013, 2007; Gould et al. 2006; Medina et al. 2013; Ping et al. 2013). Lichens were sampled in 24 sites concentrated in northeastern Puerto Rico (fig. 11). These plots are representative of eight forest types: elfin woodland, sierra palm forest, palo colorado forest, tabonuco forest, lowland moist forest, dry forest, mangrove forest and *Pterocarpus* forest (Gould et al. 2006). Surveys were made in three replicate areas for each forest type (24 sites).

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[5] Lücking, R. 2013. Personal observation.

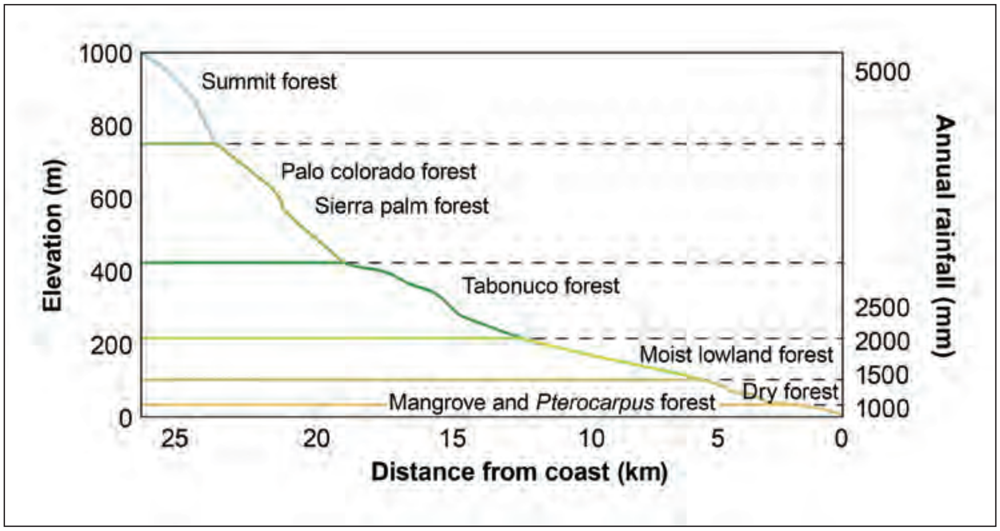

Figure 10—Sequence of eight forest types along a gradient of elevation, rainfall, and distance from the coast in northeastern Puerto Rico.

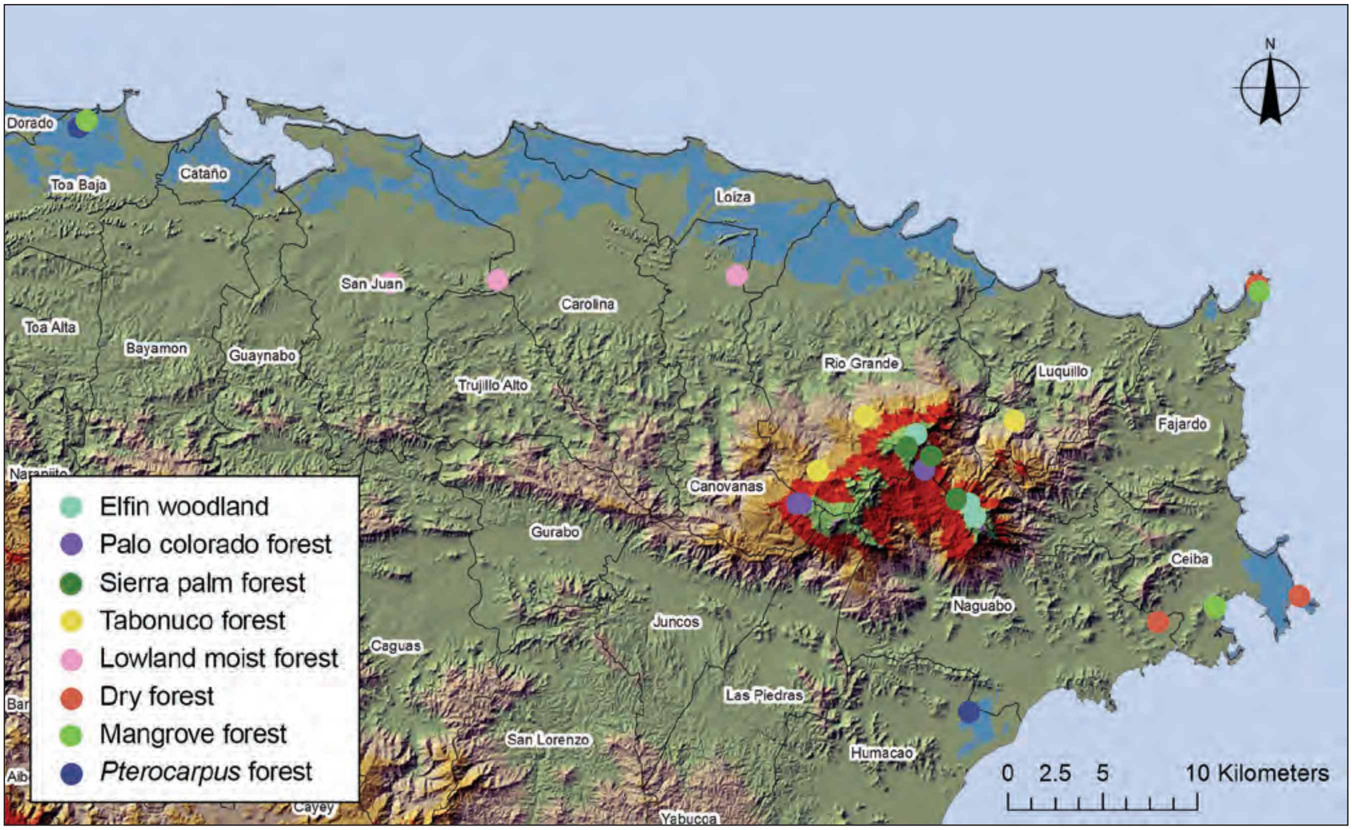

Figure 11—Location of the 24 sampling sites in northeastern Puerto Rico where lichen collecting activities for this study were completed.

Sampling Scheme

Corticolous lichens were collected in sampling sites following a nonquantitative opportunistic sampling method (Cáceres et al. 2008). Because plots used for the present study are intentionally located far from widely used trails in areas of homogeneous forest cover representative of particular ecosystems (Gould et al. 2006), lichen collection followed a slightly different approach than was used by Sipman (1996) and Cáceres et al. (2008), in which lichen collecting efforts were concentrated on main trails and occasionally at points within the forest. In this respect, information about lichen communities presented here corresponds to forest ecosystems with continuous canopy cover, which represent the vast majority of the forested land area of Puerto Rico (Brandeis and Turner 2013). Nonetheless, to partly compensate for the apparent underrepresentation of the lichens present in open areas in these forests, lichens were also collected around canopy openings commonly encountered during collecting activities. This additional information was used to supplement the descriptions of lichen communities presented in subsequent sections.

Lichen surveys were similar in practice to the nonquantitative opportunistic sampling strategy used by Cáceres et al. (2008). Trees were approached both randomly and subjectively depending on visual identification of conspicuous lichen thalli. Each tree was inspected for 3 to 5 minutes and specimens were collected for each lichen thallus recognized as a different species in each tree. From 20 to 60 trees were inspected at each site and between 50 to 100 lichen samples were collected per locality. Sampling was limited to first 0 to 2.5 m of each tree, and specimens were also collected from woody vines and areal roots available within this range. Collecting efforts stopped after 10 minutes passed without encountering new species. This “species saturation” time varied significantly between sites. For example, in mangrove forests, most of the species were collected before 30 minutes had passed; however, in palo colorado and tabonuco forests, 2 hours may have passed without reaching species saturation. Specimens were taken to the Multipurpose Laboratory at the International Institute of Tropical Forestry and identified using microscopic techniques and spot tests (Brodo et al. 2001, Orange et al 2010). Additional identification of difficult taxa was done in laboratory facilities of the Field Museum, Chicago. Information about lichens for each forest type was organized and manipulated in Microsoft Excel® tables.[6] PC-ORD™ v. 5.32 (MjM Software Design 1999) was used to generate ordinations based on species and genus composition (not presented in this report) that helped in visualizing general patterns of community organization and revealing factors that may explain variability between forest types.

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[6] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

Although nonquantitative opportunistic sampling may fail to detect rare, inconspicuous, sterile, or cryptic species and therefore may result in an underestimation of the real lichen diversity in these forests (Cáceres et al. 2008), the use of this approach in this study is justified mostly because our primary goal is to provide a general view of the most conspicuous elements and characteristics of the lichen flora of different forest types in Puerto Rico. Nevertheless, we strongly endorse additional efforts that use more rigorous quantitative methods to estimate lichen diversity in the island. Hopefully, this study will stimulate the formation of new initiatives that will move further research in that direction.

The diversity of thelotremoid lichens in a forest can provide valuable information about its conservation status.

Forest Health and Thelotremoid Lichens

Lichens could potentially provide valuable information about the conservation status of tropical forests. A recent study found that the number of morphotypes of taxa belonging to **thelotremoid** Graphidaceae is correlated with different levels of ecological continuity in these forests (Rivas-Plata et al. 2008). An easy-to-implement sampling protocol, in which thelotremoid lichens are used to assess disturbance levels of tropical forest sites based on the Index of Ecological Continuity (IEC), was also proposed (Rivas-Plata et al. 2008). In the context of their method, IEC could be a measure of morphotype richness depending on ecological continuity.

The method consists of establishing 500-m transects in forest areas to be studied. The number of thelotremoid morphotypes present in a number of trees along the transect is recorded. Finally, an IEC is calculated for the forest area studied by using the following formula: IEC = 100 × n/Nmax. In this formula, n = number of morphotypes per site, and Nmax = maximum expected number of morphotypes per site. There are 24 properly described thelotremoid morphotypes (fig. 12). Morphological characters of these morphotypes are described in table 1.

The most critical element of the IEC is the setting of Nmax, which has to be adjusted to the forest ecosystem (Rivas-Plata et al. 2008). Although Rivas-Plata et al. (2008) provided Nmax values for most of the forest conditions to be found between an altitudinal range of 0 to 3500 m in tropical America, the information was derived from a dataset from Costa Rica, a continental area not affected by the mass elevation effect, a meteorological phenomenon that lowers altitudinal zones in island ecosystems (Grubb 1971). Thus, the direct use of Rivas-Plata et al. (2008) Nmax values in IEC calculations for forests in Puerto Rico would suppose an underestimation of ecological continuity. Altogether, these observations highlight the importance of making corrections to Nmax values for insular regions.

A list of the total number of thelotremoid morphotypes found in the three sampled areas for each forest ecosystem treated in this study is presented at the

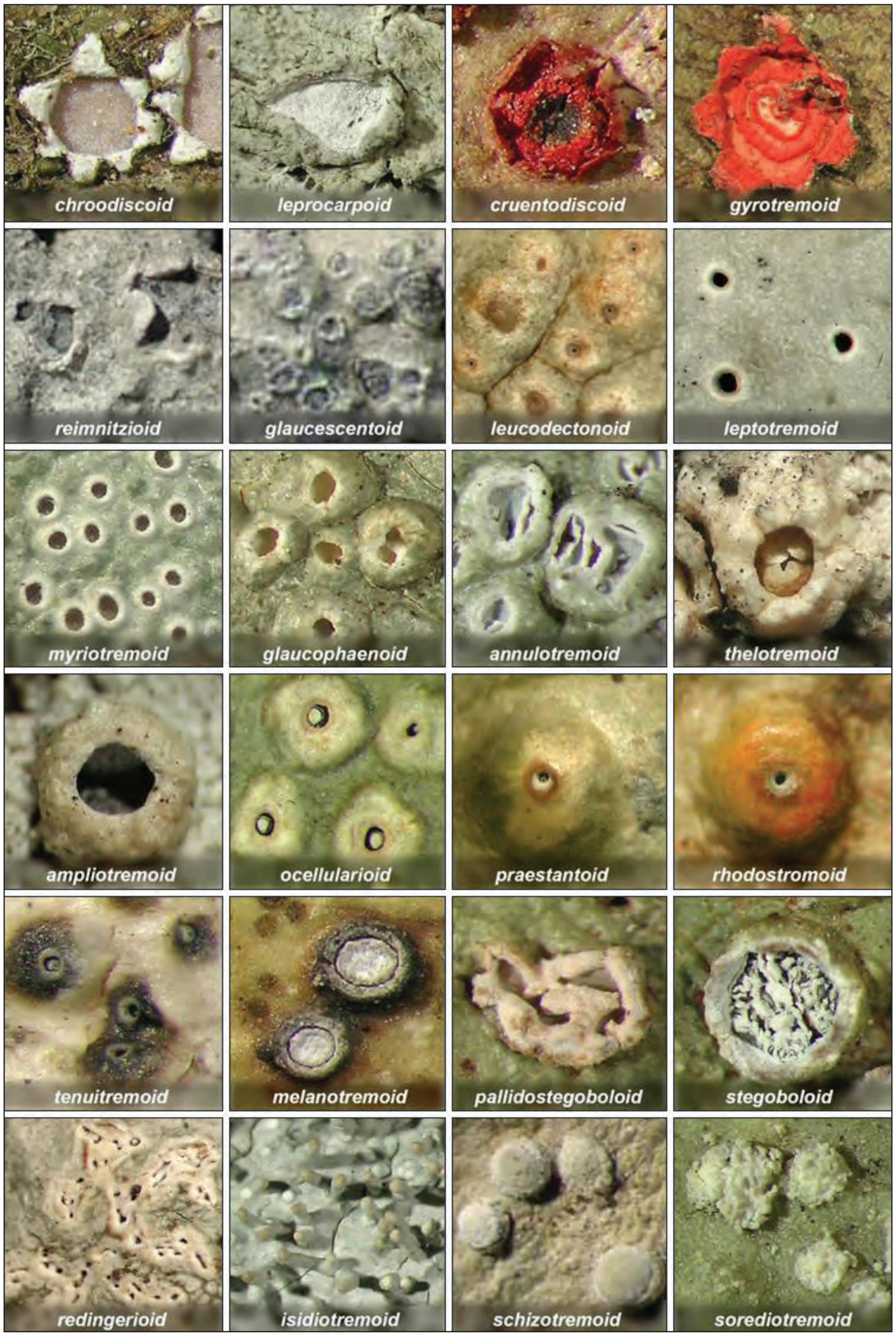

Figure 12—Morphotypes of corticolous thelotremoid lichens.

Table 1—Morphological characteristics of corticolous thelotremoid lichens (modified from Rivas-Plata et al. 2008)

Morphotype	Apothecia and reproductive structures	Thallus[a]	Genera
Chroodiscoid	Open with recurved lobules	Smooth, ± shiny	*Acanthotrema*, *Chapsa*
Leprocarpoid	Open with erect lobules	Mealy, ± matte	*Chapsa*
Cruentodiscoid	Open with erect lobules, disc pigmented	Smooth, ± shiny	*Chapsa*
Gyrotremoid	Open with recurved lobules, disc, pigmented with concentric rings	Smooth, ± shiny	*Gyrotrema*
Reimnitzioid	Open with erect lobules	Rough, with crystals	*Reimnitzia*
Glaucescentoid	Open with erect lobules	Rough, with crystals	*Leucodecton glaucescens*
Leucodectonoid	Closed with a tiny pore	Rough, with crystals	*Leucodecton*
Leptotremoid	Immersed with small pore	Rough, with crystals	*Leptotrema*
Myriotremoid	Immersed with small pore	Smooth, ± shiny	*Myriotrema* (glaucopallens group)
Glaucophaenoid	Prominent with wide pore, in section with pale walls	Smooth, ± shiny	*Myriotrema*
Annulotremoid	Prominent with wide pore, pore with inner ring	Smooth, ± shiny	*Myriotrema*, *Thelotrema*
Thelotremoid	Prominent with wide pore and inner “mouth”	Smooth, ± shiny	*Thelotrema*
Ampliotremoid	Prominent with wide pore, in section with black walls	Smooth, ± shiny	*Ampliotrema*, *Ocellularia*
Ocellularioid	Prominent with wide pore, pore with “finger” (columella), in section with black walls	Smooth, ± shiny	*Ocellularia*
Praestantoid	Large and prominent with small pore, pore with “finger” (columella), in section with black walls	Smooth, ± shiny	*Ocellularia* (*praestans* group)
Rhodostromoid	Large and prominent with small pore, pore with “finger” (columella), in section with black walls and pigment	Smooth, ± shiny	*Ocellularia* (*rhodostroma* group)
Tenuitremoid	Immersed with small pore and black margin, pore with “finger” (columella), in section with black walls	Smooth, ± shiny	*Clandestinotrema*
Melanotremoid	Prominent with wide pore and black margin, pore filled with broad “stump” (columella), in section with black walls	Smooth, ± shiny	*Melanotrema*, *Ocellularia*, *Clandestinotrema*, *Trinathotrema*
Pallidostegoboloid	Prominent with wide pore, pore filled with irregular structures, in section with pale walls	Smooth, ± shiny	*Stegobolus* (*wrightii* group)
Stegoboloid	Prominent with wide pore, pore filled with irregular structures, in section with black walls	Smooth, ± shiny	*Stegobolus*
Redingerioid	Immersed with linear slit, slit filled with irregular structures, in section with black walls	Smooth, ± shiny	*Redingeria*, *Stegobolus*
Isidiotremoid	Apothecia lacking, with isidia	Smooth, ± shiny	*Myriotrema*, *Ocellularia*
Schizotremoid	Apothecia lacking, with schizidia	Smooth, ± shiny	*Stegobolus*
Sorediotremoid	Apothecia lacking, with soralia	Smooth, ± shiny	*Myriotrema*, *Ocellularia*

[a] The symbol “±” is used here to mean “more or less.”

end of each “Lichen Community” subsection. This information should aid in the correct determination of appropriate Nmax values to be used in future IEC calculations for Puerto Rican forests. Suitable Nmax values are fundamental for the effective use of the methods proposed by Rivas-Plata et al. (2008) and simplified by Mercado-Díaz et al. (N.d).[7]

Organization and Other Considerations

Each section describing forest types in this report has three main subsections. The first, Environment, offers a general description of the physical environment of each forest type. This includes information on mean annual temperature, mean annual precipitation, and elevation range in which this type of forest is found on the island. The second section, Vegetation, aims to briefly illustrate the main aspects of vegetation composition and structure in these forests. This information is important because vegetation surfaces ultimately provide the substrate on which most of the lichen species present in the forest understory grow. The third section is titled Lichen Communities; its main purpose is to describe general characteristics of lichen communities in these forests. Information presented in this section include (1) observations about the abundance and richness of the different species and genera; (2) descriptions of commonly found growth forms, genera and species, (3) accounts of species that were found only in some of these forests; and (4) other ecological observations concerning the interaction between lichen communities and particular forest elements, e.g., lichen species occurrences in particular tree species. Each section is supplemented with photographs that illustrate common views of forest types and other vegetation attributes found in these forests.

Bound into the center of this volume is a set of species plates, which contain images of the lichen species mentioned in the “Lichen Communities” subsection of each forest type. The species names followed by an asterisk (*) indicate that the photograph was taken in the field with a high-resolution digital camera. The rest of the images were taken with a digital camera mounted on a stereomicroscope. To detect the detailed morphological characters shown in these images, and consequently facilitate field identification, the use of a 10× hand lens is recommended. It should be noted that photographs taken with the stereomicroscope are of herbarium specimens. Specimens in herbarium conditions are dry and usually have less vivid colors than species growing in their natural habitats; therefore, care should be taken when using these images for identification purposes.

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[7] Mercado-Díaz, J.A.; Gould, W.A.; González, G.; Torres-Santana, C. [N.d]. Using lichens as indicators of forest health in Puerto Rico. Manuscript in preparation. On file with: J.A. Mercado-Díaz, U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry, Jardin Botanico Sur, 1201 Calle Ceiba, San Juan, PR 00926-1119.

Note that although lichens were surveyed exhaustively at each site, the number of species reported for each ecosystem is not thought to be definitive. Additional lichen surveys in other areas will likely increase the number of species for a particular ecosystem. Species richness is reported with the main purpose of offering a general view of the diversity of lichens that a person sampling a similar area of a particular forest type might find. Likewise, the information related to the species and genera found exclusively in a particular ecosystem is tentative. Subsequent field surveys in other forests should likely reveal the presence of many of these species and genera elsewhere.

Some information presented throughout this report concerning lichen species occurrences in different areas of Puerto Rico and general notes about the island's lichen diversity are personal observations made by Joel A. Mercado-Díaz.

Forests

Puerto Rico has an extremely rich diversity of forests. This diversity could be explained by the role that a number of environmental and historical factors have had on the ecological processes shaping these ecosystems (Lugo 2005). There are numerous schemes that have been used to describe these forests; however, many of them lack a comprehensive description of their ecology (Lugo 2005).

The following sections aim to broaden the ecological knowledge of eight forest ecosystems of Puerto Rico by presenting information on their abiotic characteristics, vegetation, and lichen communities. These ecosystems are elfin woodland, palo colorado forest, sierra palm forest (fig. 13), tabonuco forest, lowland moist forest, dry forest, mangrove forest, and *Pterocarpus* forest. Many ecological aspects of these forests and the sampled sites have been described previously (González et al. 2007, Gould et al. 2006) and are the object of ongoing ecological research (González et al. 2013).

Elfin Woodland

Environment—

The elfin woodland forest type (fig. 14) occurs within the two wettest Holdridge life zones of Puerto Rico, the lower montane wet and rain forests. The elfin woodland has an approximate mean annual precipitation of 3908 mm and a mean annual temperature of 19.5 °C (Gould et al. 2006). This forest type occupies very little area in Puerto Rico, occurring in a single crescent-shaped band on the windward faces of the Luquillo Mountains (Miller and Lugo 2009). The approximate elevation of this forest type within El Yunque National Forest is 1010 m (Gould et al. 2006). Owing to the superabundance of water, soils are at field capacity much of the year and the


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Figure 13—A fire ant walking over a gelatinous-foliose lichen of the genus *Leptogium* in a sierra palm forest, El Yunque National Forest, Puerto Rico.


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Figure 14—The understory of an elfin woodland forest in El Yunque National Forest, Puerto Rico.

total annual runoff (3400 mm) is more than twice the annual rainfall input received by most areas of the world (Miller and Lugo 2009). Because the elfin woodland ecosystem of Puerto Rico lies entirely within El Yunque National Forest, the whole forest type is legally protected.

Vegetation—

The elfin woodland is a closed broad-leaved evergreen forest that generally occurs in exposed areas and ridges and is characterized by twisted, gnarled trees that are less than 7 m tall, with small diameters, a large number of stems per unit area, and extremely slow growth rates (Gould et al. 2006, Miller and Lugo 2009) (fig. 15). All trees have sclerophyllous leaves that tend to be grouped near the ends of the branches (Miller and Lugo 2009). Common trees found in this forest include *Ocotea spathulata* Mez., *Eugenia borinquensis* Britton, *Tabebuia rigida* Urb., *Magnolia splendens* Urb., and *Clusia rosea* Jacq.; whereas rare endemic tree species include *Ardisia luquillensis* (Britton) Alain and *Ilex obcordata* Sw. var. *obcordata* (Gould et al. 2006, Miller and Lugo 2009). This forest type is also characterized by its superabundance of nonvascular epiphytes, particularly mosses and liverworts, and the presence of lianas like the endemic *Marcgravia sintenisii* Urb. and *Mikania cordifolia* (L. f.) Willd. (Gould et al. 2006, Lugo 2005). Refer to table 2 for common names of plant species identified in this report.

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Figure 15—Species of *Clandestinotrema* growing on an upright branch of a tree in an elfin woodland forest, El Yunque National Forest, Puerto Rico.

Table 2—Common names of plant species identified in this report

Scientific name	Common name in English	Common name in Spanish (Puerto Rican usage)
Acrostichum aureum	Golden leather fern	Palmita del rio
Alchornea latifolia		Achiotillo
Ardisia luquillensis	Mountain marlberry	Mameyuelo
Avicennia germinans	Black mangrove	Mangle negro
Bourreria succulenta	Bodywood	Palo de vaca
Bursera simaruba	Gumbo limbo	Almácigo
Byrsonima wadsworthii		Almendrillo
Cecropia schreberiana	Pumpwood	Yagrumo hembra
Clusia rosea	Scotch attorney	Cupey
Conocarpus erectus	Button mangrove	Mangle boton
Cordia borinquensis		Capa cimarron
Cyathea arborea	West Indian tree fern	Helecho arboreo
Cyrilla racemiflora	Swamp titi	Palo colorado
Dacryodes excelsa	Candle tree	Tabonuco
Erythroxylum brevipes	Brisselet	Rocío
Eugenia biflora	Blackrodwood	Hoja menuda
Eugenia borinquensis		Guayabota de sierra
Faramea occidentalis	False coffee	Cafeillo
Henriettea squamulosum		Camasey jusillo
Hippocratea volubilis	Medicine vine	Bejuco prieto
Hymenaea courbaril	Stinkingtoe	Algarrobo
Ilex obcordata var. *obcordata*		Cuero de sapo
Inga laurina	Sacky sac bean	Guama
Ipomoea triloba	Little bell	Bejuquillo de puerco
Laguncularia racemosa	White mangrove	Mangle blanco
Magnolia splendens		Laurel sabino
Manilkara bidentata	Bulletwood	Ausubo
Marcgravia sintenisii	Shingleplant	Pegapalma
Mikania cordifolia	Florida Keys hempvine	Guaco
Neea buxifolia	Saltwood	
Ocotea leucoxylon	Loblolly sweetwood	Laurel geo
Ocotea spathulata		Cabalonga cimarrona
Paullinia pinnata	Bread and cheese	Bejuco de costilla
Prestoea acuminata var. *montana*	Sierran palm	Palma de sierra
Pterocarpus officinalis	Dragonsblood tree	Palo de pollo
Quadrella cynophallophora	Jamaican caper	Burro prieto
Rhizophora mangle	Red mangrove	Mangle rojo
Rondeletia portoricensis		Juan Tomás
Sloanea berteroana	Bullwood	Motillo
Spathodea campanulata	African tulip tree	Tulipán africano
Tabebuia rigida		Roble de sierra
Tetragastris balsamifera		Masa

Lichen communities—

Elfin woodlands are characterized for having low species richness of corticolous lichens if compared to other forest types in El Yunque National Forest. Only 33 species have been recorded in sampled areas of this forest type. Nonetheless, these forests have the highest number of species within the genus *Clandestinotrema*, and a good representation of taxa belonging to the genus *Chapsa*. As mentioned before, the presence of *Clandestinotrema* species in Neotropical forests is positively correlated with elevation (Rivas-Plata et al. 2008), which agrees with the observations reported here. Competition for space appears to be a major constraint for lichen colonization in the elfin woodland as bryophytes are more adapted to the high-moisture conditions found in this ecosystem.

Although most of the lichen flora in this forest adopts a crustose growth habit, it is not uncommon to find species with fruticose or squamulose growth forms, like *Cladia aggregata* (plate 1A) and *Cladonia* spp., growing on tree branches in the understory of this forest type. Foliose lichens are scarce and, if present, are most likely cyanobacterial such as species of *Leptogium*. *Dictyonema sericeum* (plate 1B) and *Cyphellostereum* (plate 1C) are examples of a filamentous **basidiolichens** present in these forests. Foliicoulous lichens are uncommon in the understory of the elfin woodland forest and nearly all species to be found are close to canopy openings.

Some of the most common lichen species found in this forest type include *Chapsa* sp. A (plate 1D), *Chapsa thallotrema* (plates 1E and 1F), *Clandestinotrema leucomelaenum* (plate 1G), *Dictyonema sericeum*, *Graphis adpressa* (plate 1H), and *Ocellularia rhodostroma* (plate 2A). Several species have only been found in sampled areas of this forest type. Some of these are *Chapsa* sp. A, *Chapsa* sp. B (plate 2B), *Cladia aggregata*, *Clandestinotrema analorenae* (plate 2C), *Clandestinotrema stylothecium* (plate 2D), *Fissurina crassilabra* (plate 2E), *Fissurina incrustans* (plate 2F), and *Graphis adpressa*.

At least six morphotypes of thelotremoid lichens have been found in elfin woodland forests in El Yunque National Forest (Rivas-Plata et al. 2008). These are the encountered morphotypes and their representative species:

Leprocarpoid: *Chapsa dissuta*
Sorediotermoid: *Chapsa thallotrema*
Tenuitremoid: *Clandestinotrema analorenae*
Melanotremoid: *Clandestinotrema leucomelaenum, C. stylothecium*
Rhodostromoid: *Ocellularia rhodostroma*
Thelotremoid: *Thelotrema porinoides*

An interesting fact from a lichenological perspective is the common sighting of free-living *Trentepohlia* spp., a filamentous green algae hanging from tree branches in the elfin woodland forest (fig. 3). *Trentepohlia* is the most common photobiont participating in lichenological associations in tropical ecosystems and is recognized by its filamentous growth habit and distinctive orange color, which is caused by the presence of carotenoid pigments that mask the green pigments of chlorophyll. In lichenized state, *Trentepohlia* loses its ability to produce carotenoids. *Trentepohlia* filaments may also be found in other areas around the island, particularly under humid and illuminated conditions.

Palo Colorado Forest

Environment—

The palo colorado forests in Puerto Rico (fig. 16) are considered "mountain wetlands" (Frangi 1983), and according to Holdridge's system (Ewel and Whitmore 1973), this forest lies within the subtropical lower montane wet forest (Gould et al. 2006, Lugo 2005, Miller and Lugo 2009). It occurs in both the eastern and central parts of the island up to the summits of some mountains that are above 1000 m (Miller and Lugo 2009). The palo colorado forest has a high cloud cover, low illumination, extreme soil saturation, and a high water table (Lugo 2005). Mean annual temperature is about 23 °C, and mean annual precipitation reaches about 2932 mm (Gould et al. 2006). This forest covers only about 1.2 percent of the island's total

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Figure 16—The understory of a palo colorado forest in El Yunque National Forest, Puerto Rico.

surface area (Weaver 1987), but encompasses nearly 17 percent of the Luquillo Mountains, and grows at elevations higher than 600 m. In El Yunque National Forest, these forests are considered cloud forests precisely because cloud condensation commonly starts at this elevation (Lugo 2005).

Vegetation—
The palo colorado forest is mostly a closed broad-leaved evergreen forest that gets its name from the presence of its common tree *Cyrilla racemiflora* L. (Gould et al. 2006) (fig. 17). This forest corresponds to mature vegetation of the zonal association in the subtropical lower montane wet forest (Miller and Lugo 2009). It is a low-statured forest (3 to 9 m) and, in some places, trees are considerably dispersed owing either to high area occupancy of large-diameter trees or because environmental conditions limit their density (Lugo 2005). Although the palo colorado forest is a closed forest, canopy openings allow light penetration. Clouds continuously penetrate the understory, which is considerably open (Lugo 2005). The palo colorado forest is poorer in plant species than the adjacent tabonuco forests (Miller and Lugo 2009). Common tree species include *Cyathea arborea* (L.) Sm., *Prestoea acuminata* (Willd.) H.E. Moore var. *montana* (Graham) A. Hend. & G. Galeano, *Ocotea spathulata*, *Alchornea latifolia* Sw., among others (Gould et al. 2006, Lugo 2005). A study classifying vegetation in these forests found about 14 endemic tree species and six rare native species in the palo colorado forests of El Yunque National Forest (Gould et al. 2006). Refer to table 2 for common names of plant species.

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Figure 17—Lichens are commonly found on aerial roots of trees in the palo colorado forest in El Yunque National Forest. In this photo: (A) *Coenogonium linkii*, and (B) *Myeloconis guyanensis.*

Plates

Species photographs in plates are organized in the order in which they are mentioned in the text. Species names followed by an asterisk (*) indicate that the photograph was taken in the field with a high-resolution digital camera. The remainder of the images were taken with a digital camera mounted on a stereomicroscope.

Plate 1
(A) *Cladia aggregata*
(B) *Dictyonema sericeum** (growing on moss)
(C) *Cyphyellostereum phyllogenum*
(D) *Chapsa* sp. A
(E) *Chapsa thallotrema**
(F) *Chapsa thallotrema** (detail)
(G) *Clandestinotrema leucomelaenum*
(H) *Graphis adpressa*.

Plate 2
(A) *Ocellularia rhodostroma*
(B) *Chapsa* sp. B
(C) *Clandestinotrema analorenae*
(D) *Clandestinotrema stylothecium*
(E) *Fissurina crassilabra*
(F) *Fissurina incrustans*
(G) *Coenogonium linkii**
(H) *Herpothallon aurantiacoflavum* (*left) and *Herpothallon granulare* (*right).

Plate 3
(A) *Herpothallon aurantiacoflavum*
(B) *Herpothallon granulare*
(C) *Dichosporidium nigrocinctum**
(D) *Dichosporidium nigrocinctum* *(*fruiting bodies)
(E) *Graphis rhizocola**
(F) *Malmidea nigromarginata*
(G) *Myeloconis guyanensis**
(H) *Ocellularia praestans**

Plate 4
(A) *Ocellularia praestans* (detail)
(B) *Porina nucula*
(C) *Ampliotrema rimosum**
(D) *Arthonia* sp. (yellow margin)
(E) *Chapsa alborosella*
(F) *Clandestinotrema* cf. *tenue*
(G) *Coenogonium nepalense*
(H) *Graphis dimidiata*.

Plate 5
(A) *Malmidea furfurosa*
(B) *Malmidea vinosa*
(C) *Paratopeliopsis caraibica*
(D) *Ocellularia* aff. *perforata*
(E) *Ocellularia cavata*
(F) *Ocellularia crocea*
(G) *Ocellularia dolichotata*
(H) *Ocellularia rhabdospora*.

Plate 6
(A) *Platythecium grammitis*
(B) *Sticta* sp.*
(C) *Leptogium azureum**
(D) *Leptogium denticulatum**
(E) *Graphis duplicata*
(F) *Porina subpungens**
(G) *Thelotrema porinoides*
(H) *Arthonia complanata**.

Plate 7
(A) *Graphis proserpens**
(B) *Fissurina* sp. nov.*
(C) *Fissurina* sp. nov. (detail)
(D) *Megalotremis lateralis*
(E) *Pyrenula* aff. *fetivica**
(F) *Sticta beauvoisii**
(G) *Porina scabrida*
(H) *Mazosia endonigra*.

Plate 8
(A) *Herpothallon rubrocinctum**
(B) *Phyllopsora buettneri*
(C) *Phyllopsora corallina**
(D) *Usnea* sp.*
(E) *Stereocaulon ramulosum**
(F) *Cladonia subradiata* *
(G) *Arthonia platygraphidea*
(H) *Arthothelium distendens*.

Plate 9
(A) *Ocellularia interposita*
(B) *Pyrenula macrocarpa*
(C) *Pyrenula massariospora**
(D) *Heterodermia speciosa*
(E) *Acanthotrema alboisidiatum*
(F) *Arthonia* aff. *bessalis*
(G) *Arthothelium* sp. nov
(H) *Pseudochapsa dilatata*.

Plate 10
(A) *Chapsa elabens*
(B) *Eugeniella* sp. nov
(C) *Herpothalon* aff. *pustulata**
(D) *Letrouitia vulpina*
(E) *Leucodecton compuctellum*
(F) *Malmidea amazonica*
(G) *Mazosia verrucosa*
(H) *Megalotremis infernalis*.

Plate 11
(A) *Ocellularia* aff. *cavata*
(B) *Ocellularia ascidiodea*
(C) *Ocellularia mordenii*
(D) *Borinquenotrema soredicarpum*
(E) *Porina americana*
(F) *Rhabdodiscus emersellus*
(G) *Wirthiotrema glaucopallens*
(H) *Coenogonium leprieurii**.

Plate 12
(A) *Physcia atrostriata**
(B) *Parmotrema praesorediosum**
(C) *Dirinaria purpurascens*
(D) *Ramalina complanata**
(E) *Ramalina peruviana**
(F) *Cresponea melanocheiloides**
(G) *Cresponea melanocheiloides* (detail)
(H) *Cryptothecia striata**.

Plate 13
(A) *Diorygma poiteai**
(B) *Diorygma poiteai* (detail)
(C) *Hemithecium balbisii**
(D) *Hemithecium balbisii* (detail)
(E) *Graphis glaucescens**
(F) *Graphis glaucescens* (detail)
(G) *Malmidea piperis**
(H) *Malmidea piperis* (detail).

Plate 14
(A) *Opegrapha bonplandii*
(B) *Opegrapha dekeselii*
(C) *Phaeographis brasiliensis*
(D) *Porina distans**
(E) *Porina distans* (detail)
(F) *Porina conspersa*
(G) *Pyrenula mamillana*
(H) *Fissurina subnitens* (between bark fissures)*.

Plate 15
(A) *Fissurina subnitens* (detail)
(B) *Anisomeridium subprostans*
(C) *Arthonia* aff. *pyrrholiza*
(D) *Arthonia bessalis*
(E) *Dyplolabia afzelii*
(F) *Letrouitia domingensis**
(G) *Letrouitia domingensis* (detail)
(H) *Leucodecton bisporum**.

Plate 16
(A) *Leucodecton bisporum* (detail)
(B) *Mazosia carnea*
(C) *Melanotrema platystomum*
(D) *Monoblastia borinquensis*
(E) *Porina tetracerae*
(F) *Psoroglaena cubensis*
(G) *Strigula phaea*
(H) *Trinathotrema stictideum*.

Plate 17
(A) *Physcia crispa*
(B) *Physcia sorediosa*
(C) *Pyxine berteriana*
(D) *Pyxine eschweileri*
(E) *Anisomeridium biforme*
(F) *Arthonia portoricensis*
(G) *Arthopyrenia majuscula*
(H) *Bactrospora denticulata*.

Plate 18
(A) *Graphis furcata*
(B) *Graphis tenella*
(C) *Opegrapha* cf. *varia*
(D) *Pyrenula quassiaecola*
(E) *Arthonia antillarum*
(F) *Arthonia caribaea*
(G) *Celothelium dominicanum*
(H) *Coenogonium aurantiacum*.

Plate 19
(A) *Coenogonium borinquense*
(B) *Enterographa multilocularis*
(C) *Fissurina tachygrapha*
(D) *Leucodecton occultum*
(E) *Opegrapha astraea*
(F) *Phaeographis inusta* (between lenticels)
(G) *Phaeographis inusta* (detail)
(H) *Pyrenula thelomorpha*.

Plate 20
(A) *Ramonia rappii*
(B) *Ramonia valenzuelana*
(C) *Parmotrema endosulphureum*
(D) *Parmotrema endosulphureum* *(*isidia and yellow medulla)
(E) *Physcia erumpens*
(F) *Pyrenula cerina**
(G) *Pyrenula cerina* (detail)
(H) *Bactrospora myriadea*.

Plate 21
(A) *Enterographa* aff. *anguinella*
(B) *Pyrenula cocoes*
(C) *Pyrenula ochraceoflava*
(D) *Pyrenula microcarpa*
(E) *Herpothallon minimum*
(F) *Porina curtula*
(G) *Arthonia* aff. *rubella*
(H) *Coenogonium dimorphicum*.

Plate 22
(A) *Coenogonium portoricense*
(B) *Crocynia gossypina*
(C) *Fissurina adscribens*
(D) *Graphis farinulenta*
(E) *Diorygma poiteai** (left) and *Graphis farinulenta* (*right)
(F) *Lecanographa lyncea*
(G) *Malmidea* aff. *coralliformis*
(H) *Schismatomma rappii*.

Plate 1

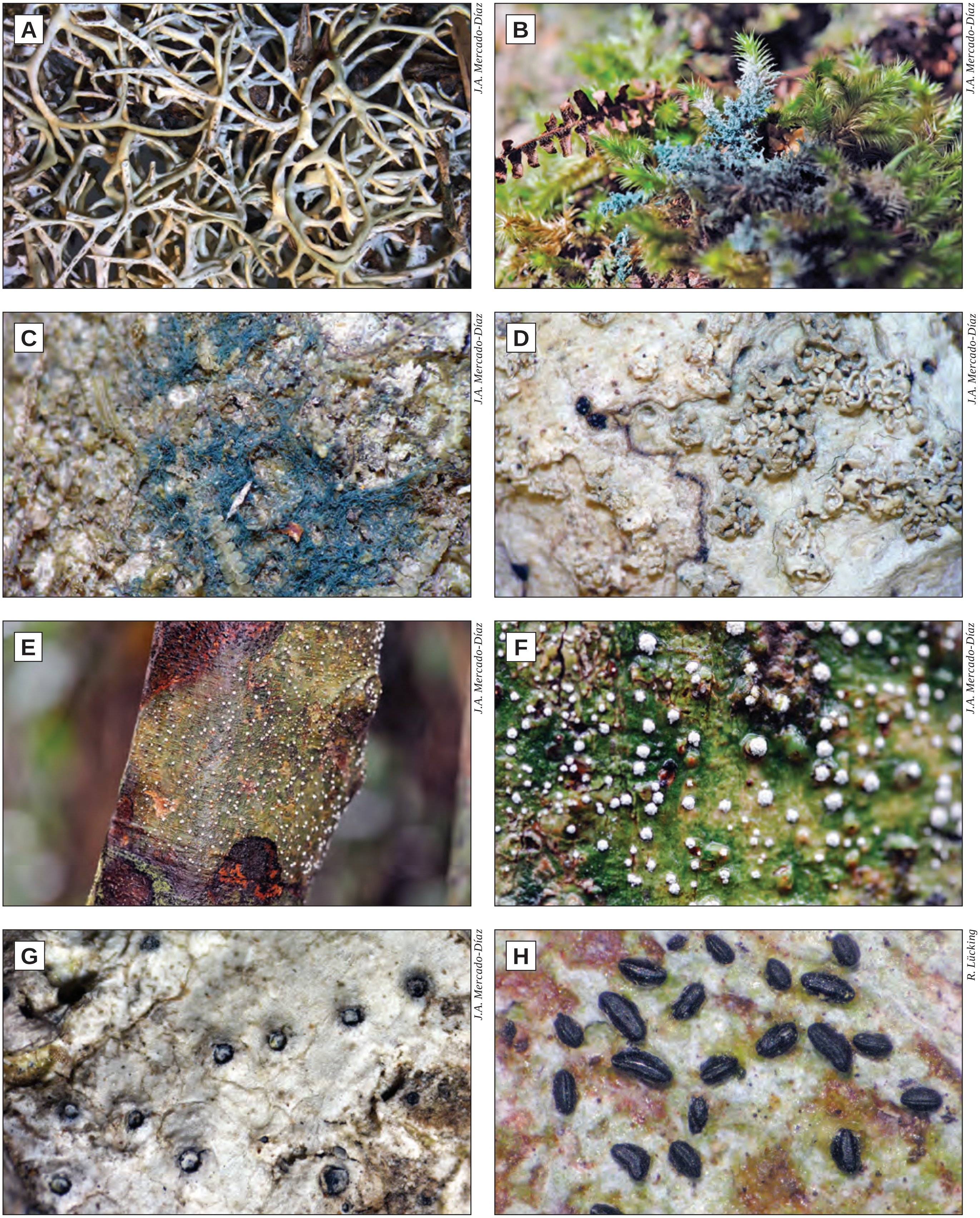

Plate 1—(A) *Cladia aggregata*; (B) *Dictyonema sericeum** (growing on moss); (C) *Cyphyellostereum phyllogenum*; (D) *Chapsa* sp. A; (E) *Chapsa thallotrema**; (F) *Chapsa thallotrema** (detail); (G) *Clandestinotrema leucomelaenum*; (H) *Graphis adpressa*.

Plate 2

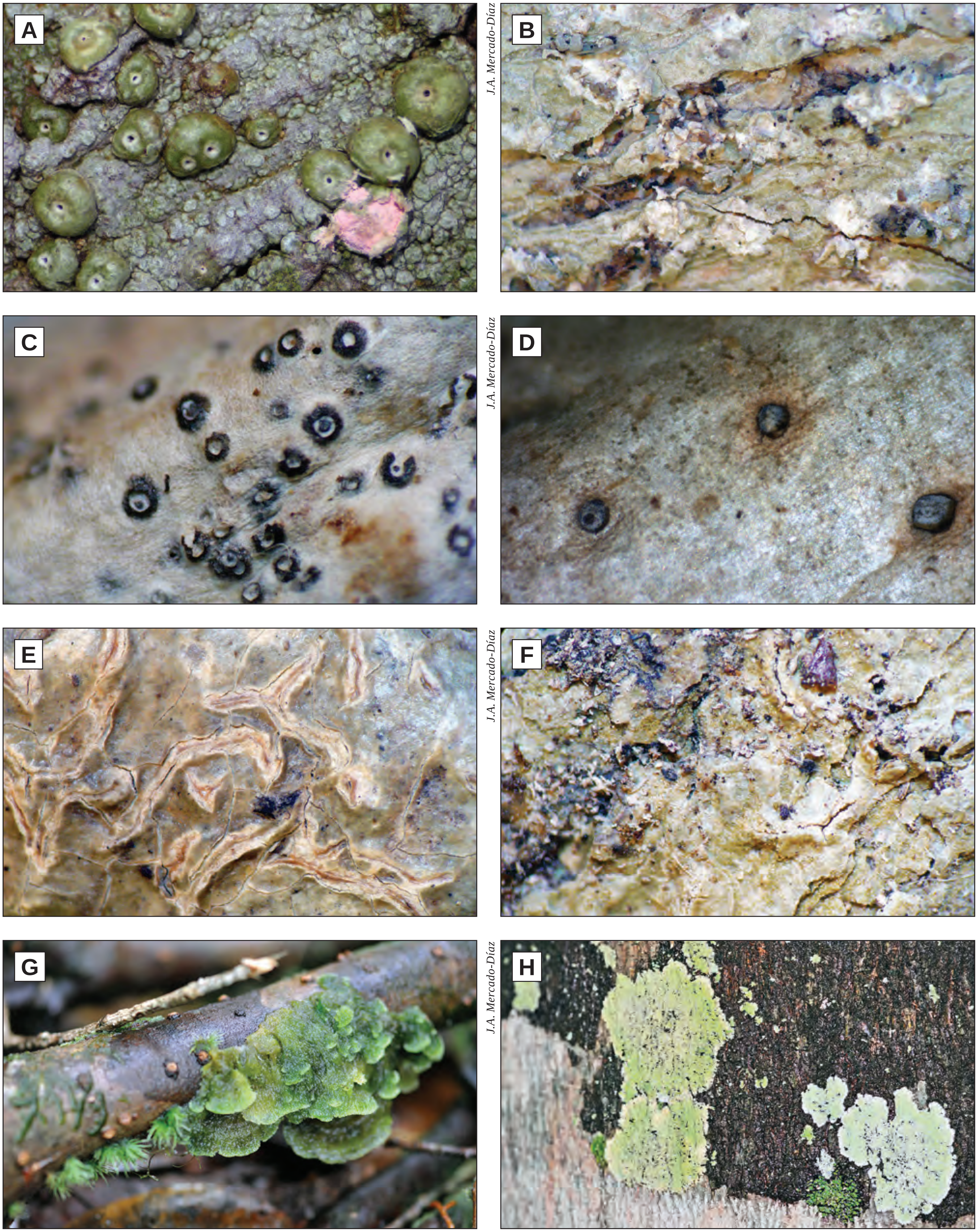

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Plate 2—(A) *Ocellularia rhodostroma*; (B) *Chapsa* sp. B; (C) *Clandestinotrema analorenae*; (D) *Clandestinotrema stylothecium*; (E) *Fissurina crassilabra*; (F) *Fissurina incrustans*; (G) *Coenogonium linkii**; (H) *Herpothallon aurantiacoflavum** (left) and *Herpothallon granulare** (right).

Plate 3

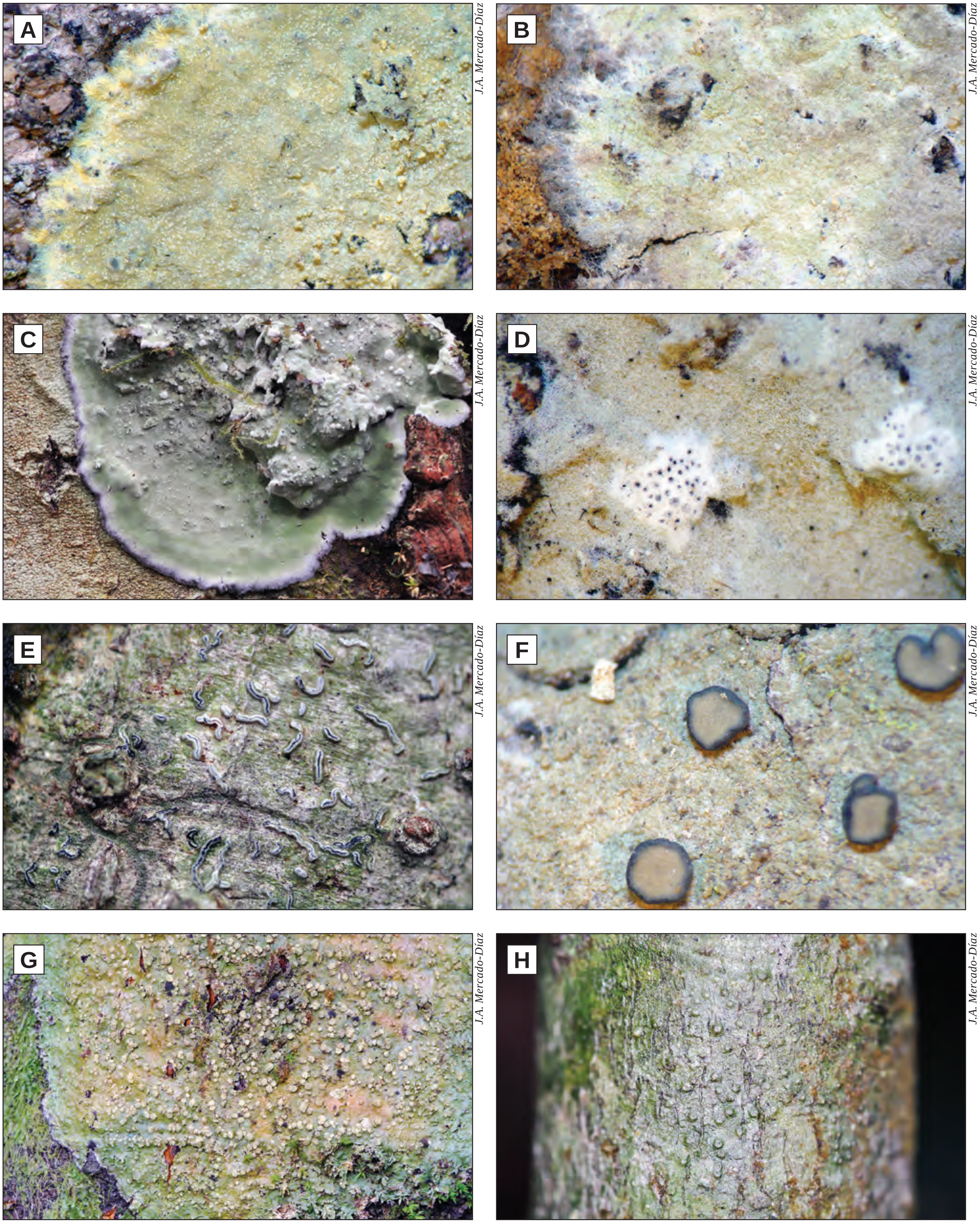

Plate 3—(A) *Herpothallon aurantiacoflavum*; (B) *Herpothallon granulare*; (C) *Dichosporidium nigrocinctum**; (D) *Dichosporidium nigrocinctum* (fruiting bodies); (E) *Graphis rhizocola**; (F) *Malmidea nigromarginata*; (G) *Myeloconis guyanensis**; (H) *Ocellularia praestans**.

Plate 4

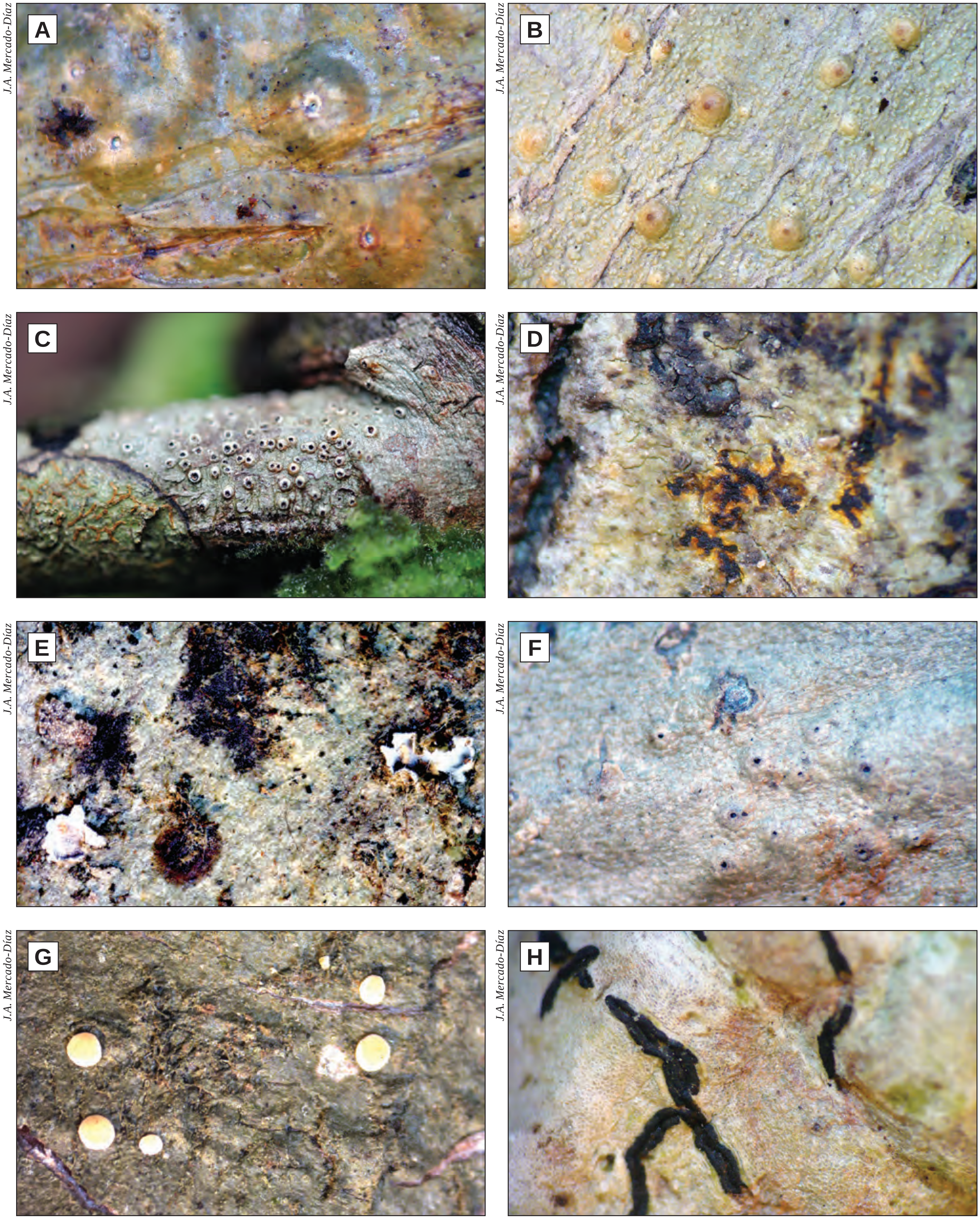

Plate 4—(A) *Ocellularia praestans* (detail); (B) *Porina nucula*; (C) *Ampliotrema rimosum**; (D) *Arthonia* sp. (yellow margin); (E) *Chapsa alborosella*; (F) *Clandestinotrema* cf. *tenue*; (G) *Coenogonium nepalense*; (H) *Graphis dimidiata*.

Plate 5

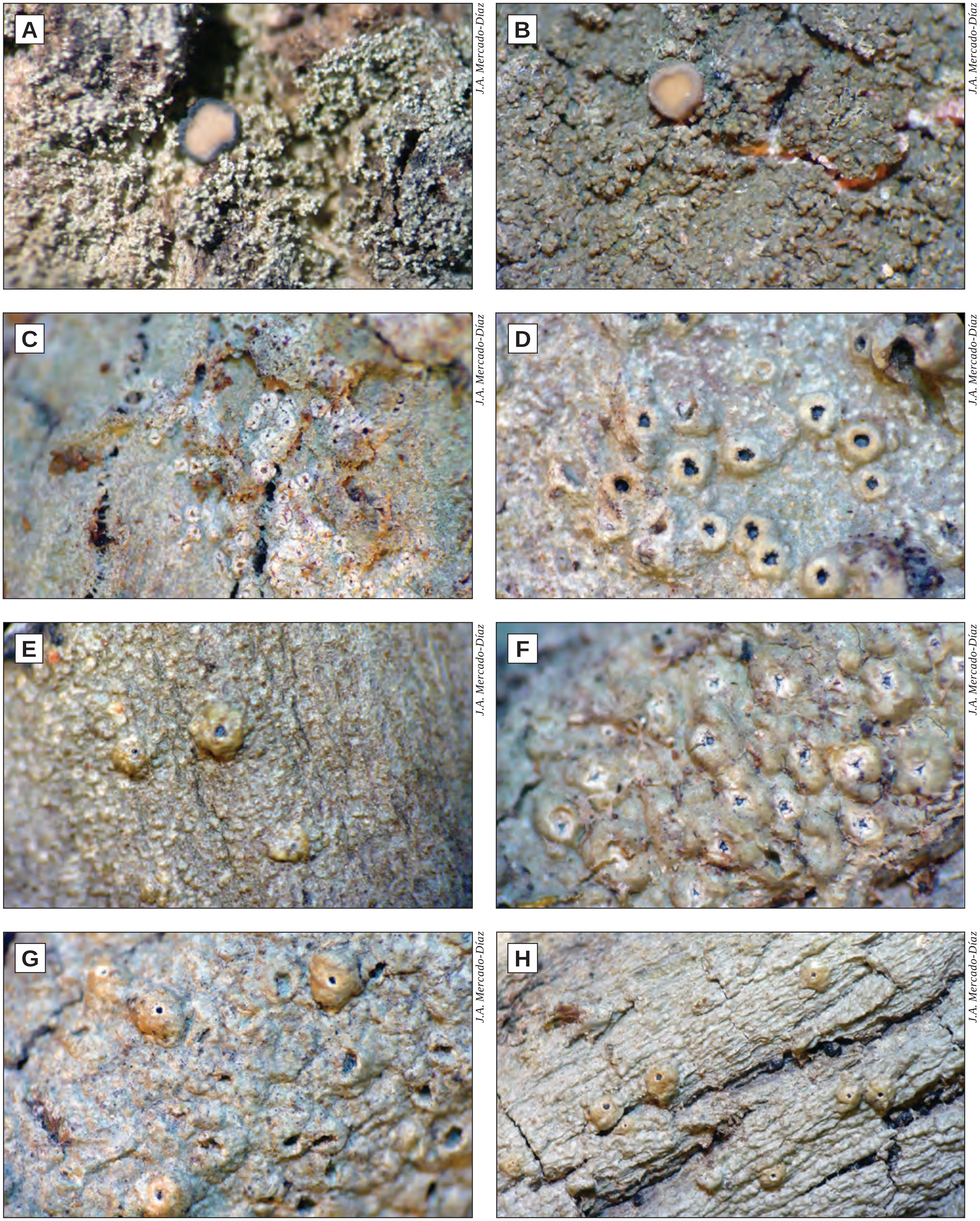

Plate 5—(A) *Malmidea furfurosa*; (B) *Malmidea vinosa*; (C) *Paratopeliopsis caraibica*; (D) *Ocellularia* aff. *perforata*; (E) *Ocellularia cavata*; (F) *Ocellularia crocea*; (G) *Ocellularia dolichotata*; (H) *Ocellularia rhabdospora*.

Plate 6

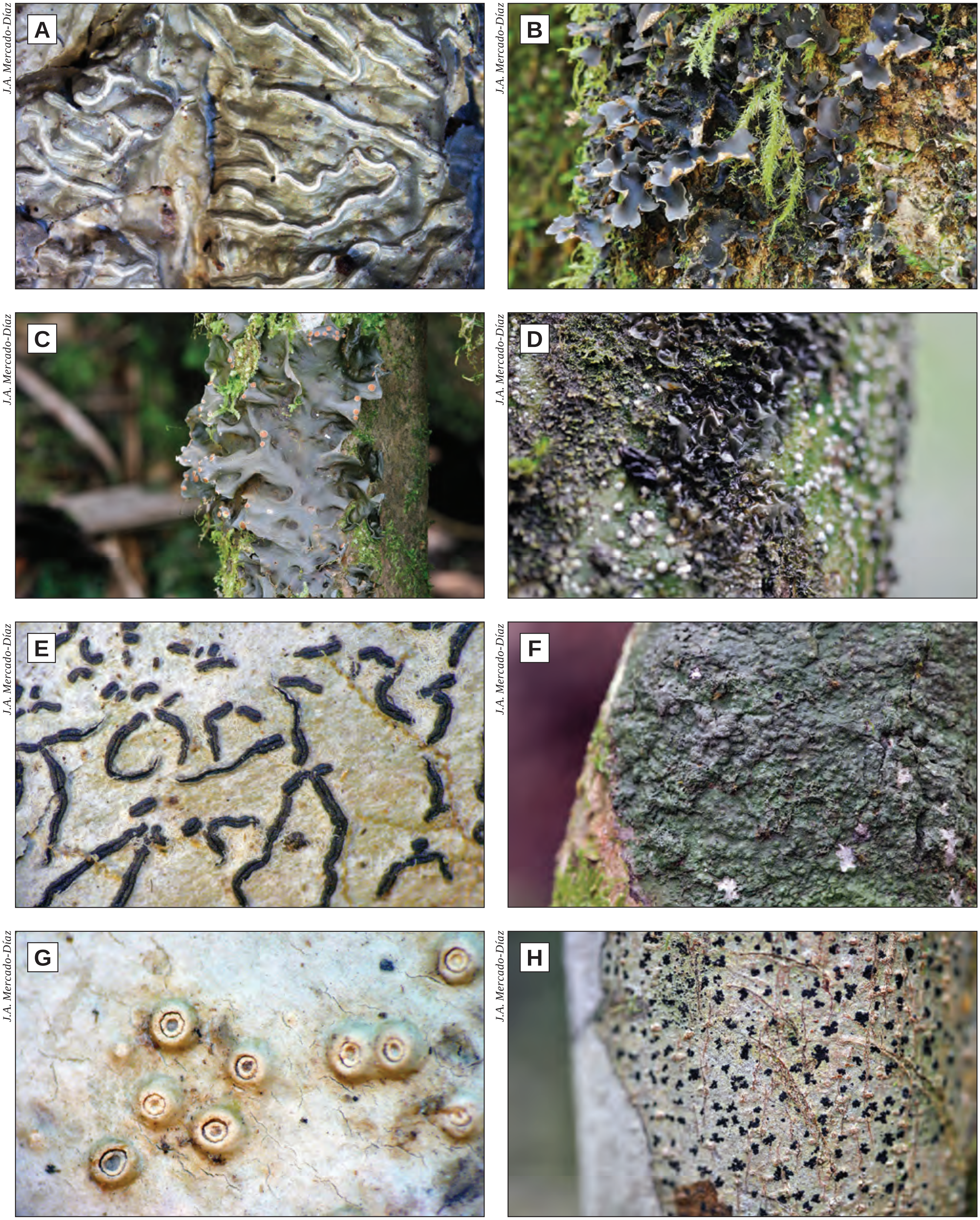

Plate 6—(A) *Platythecium grammitis*; (B) *Sticta* sp*; (C) *Leptogium azureum**; (D) *Leptogium denticulatum**; (E) *Graphis duplicata*; (F) *Porina subpungens**; (G) *Thelotrema porinoides*; (H) *Arthonia complanata**.

Plate 7

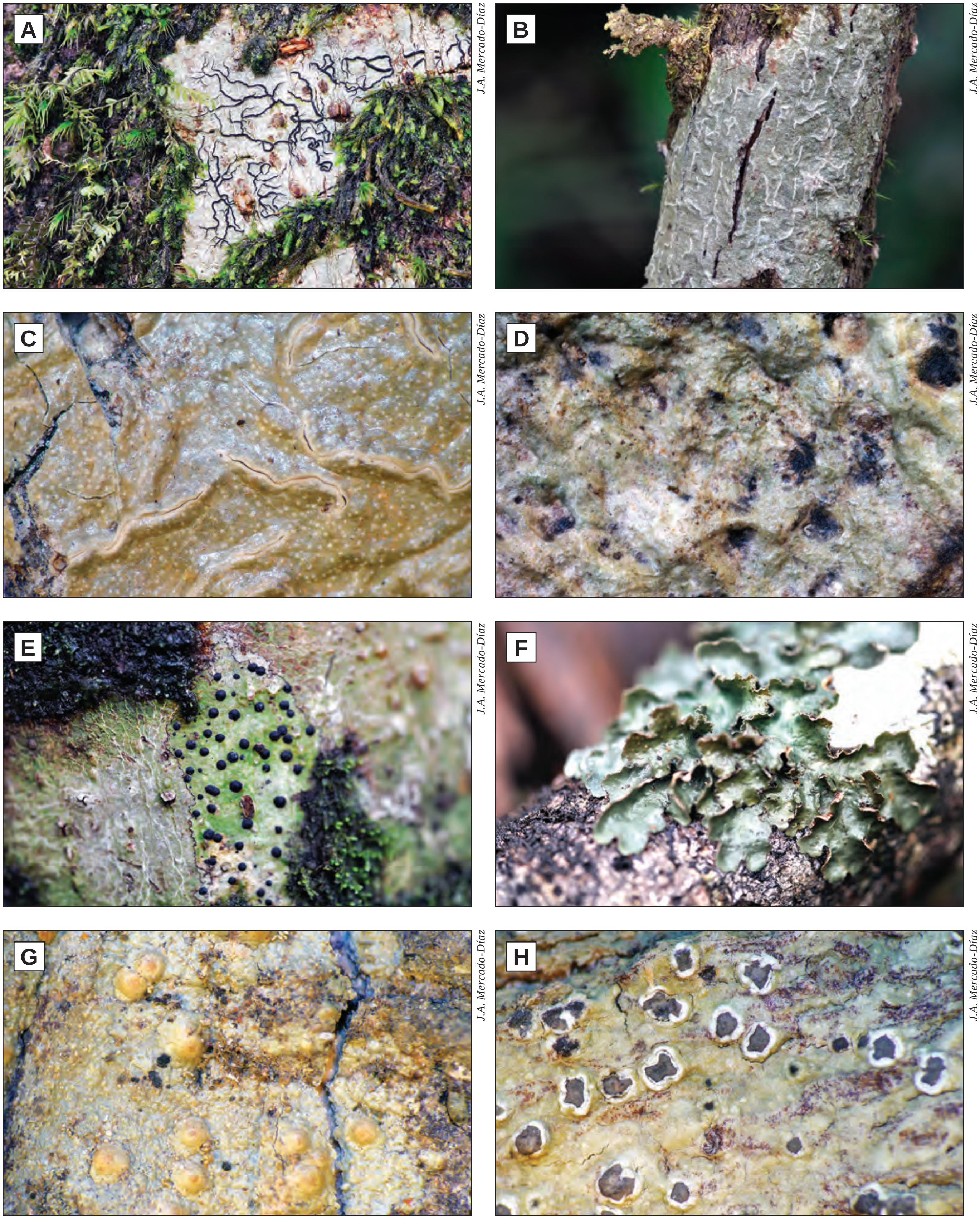

Plate 7—(A) *Graphis proserpens**; (B) *Fissurina* sp. nov.*; (C) *Fissurina* sp. nov. (detail); (D) *Megalotremis lateralis;* (E) *Pyrenula* aff. *fetivica*;* (F) *Sticta beauvoisii**; (G) *Porina scabrida*; (H) *Mazosia endonigra.*

Plate 8

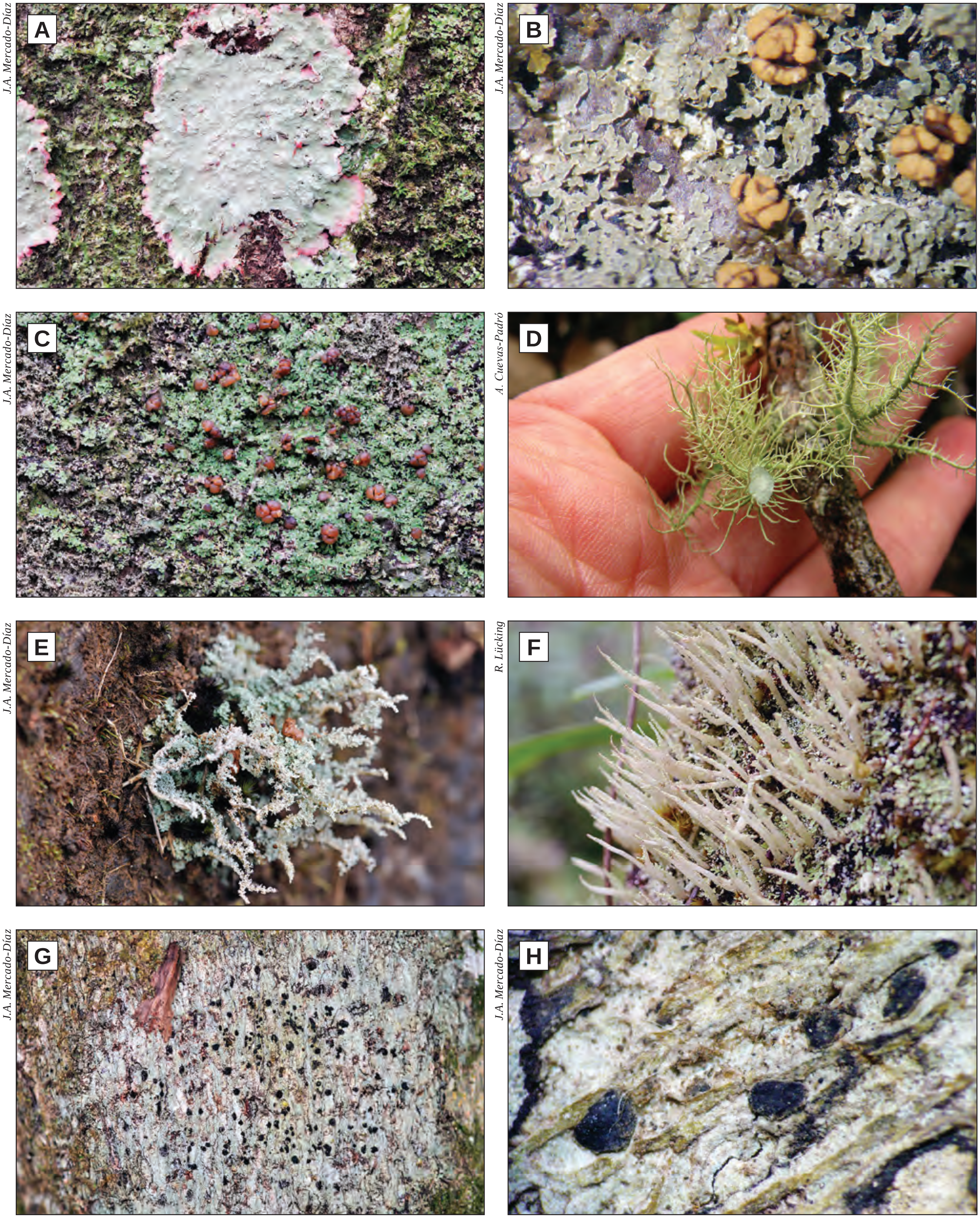

Plate 8—(A) *Herpothallon rubrocinctum**; (B) *Phyllopsora buettneri*; (C) *Phyllopsora corallina**; (D) *Usnea* sp.*; (E) *Stereocaulon ramulosum**; (F) *Cladonia subradiata* *; (G) *Arthonia platygraphidea*; (H) *Arthothelium distendens.*

Plate 9

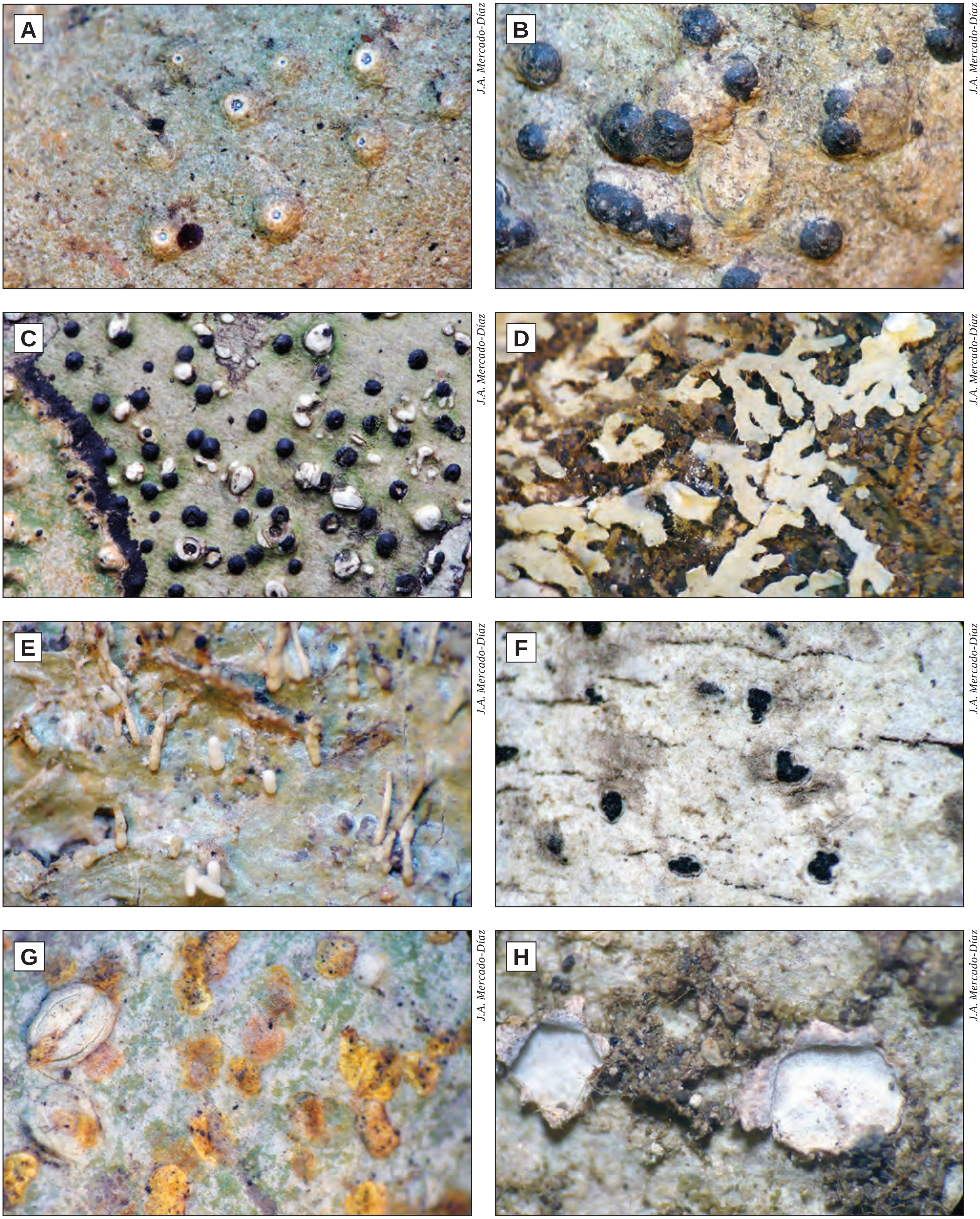

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Plate 9—(A) *Ocellularia interposita*; (B) *Pyrenula macrocarpa*; (C) *Pyrenula massariospora**; (D) *Heterodermia speciosa*; (E) *Acanthotrema alboisidiatum;* (F) *Arthonia* aff. *bessalis*; (G) *Arthothelium* sp. nov; (H) *Pseudochapsa dilatata*.

Plate 10

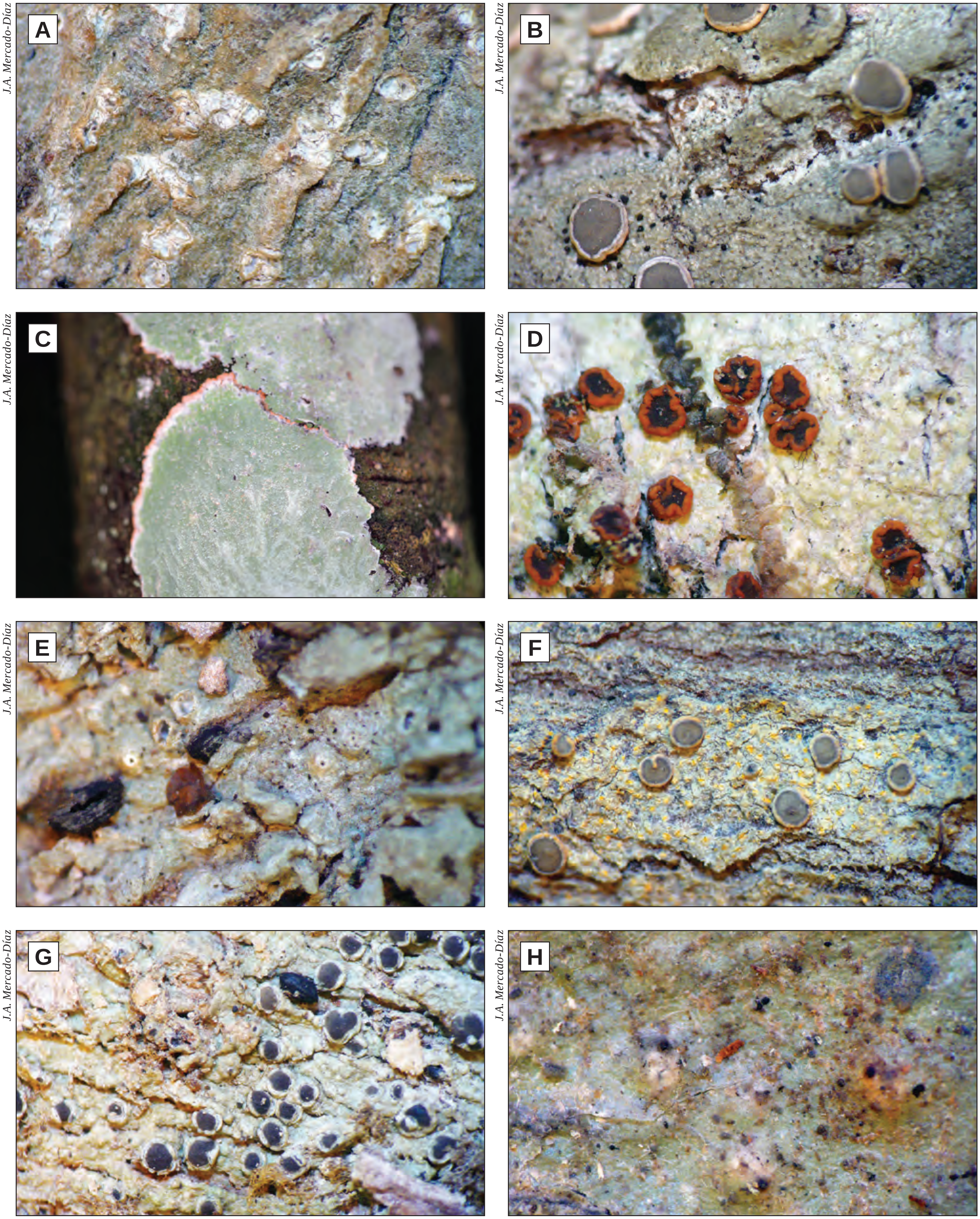

Plate 10—(A) *Chapsa elabens*; (B) *Eugeniella* sp. nov; (C) *Herpothalon* aff. *pustulata**; (D) *Letrouitia vulpina*; (E) *Leucodecton compuctellum*; (F) *Malmidea amazonica*; (G) *Mazosia verrucosa*; (H) *Megalotremis infernalis.*

Plate 11

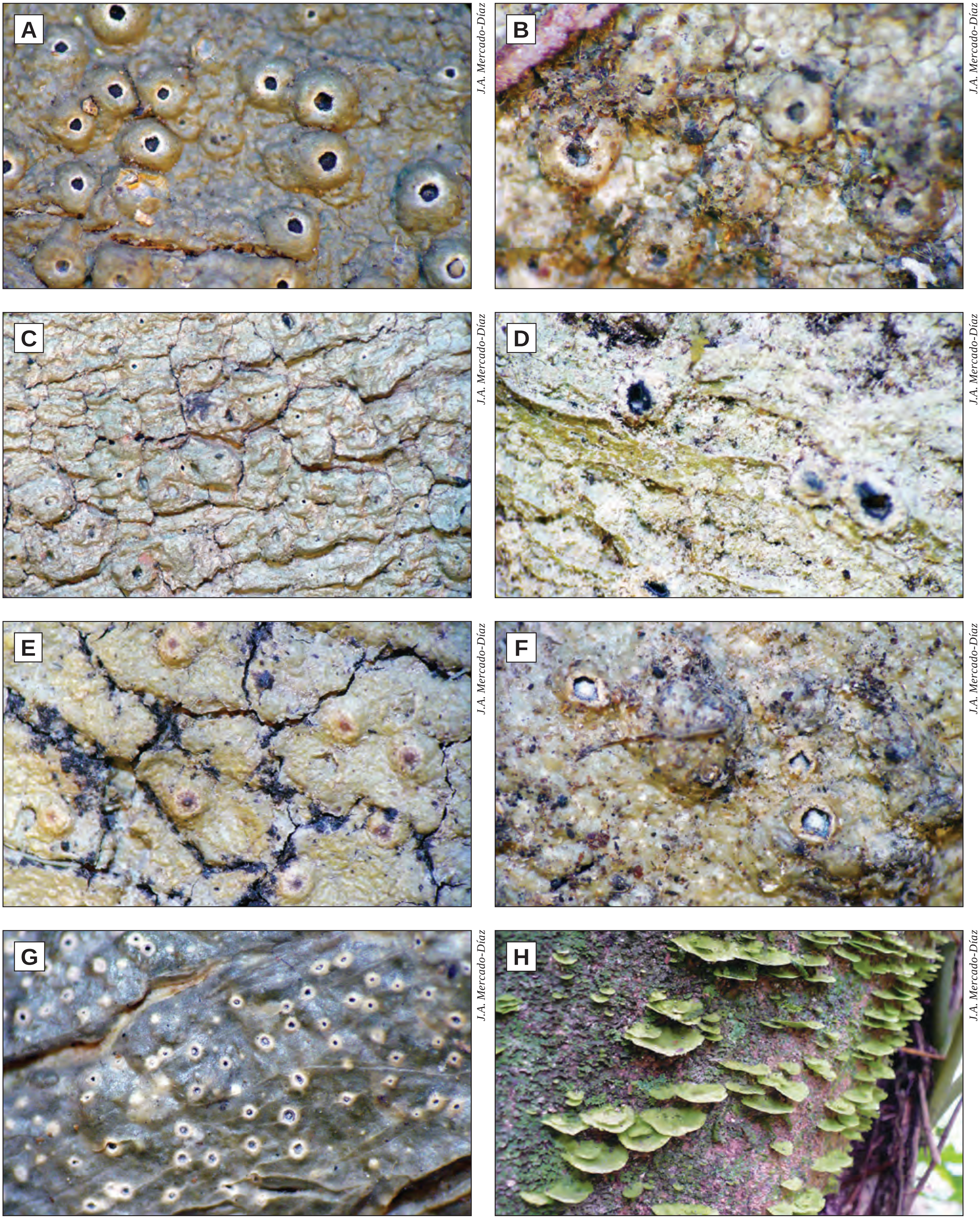

Plate 11—(A) *Ocellularia* aff. *cavata*; (B) *Ocellularia ascidiodea*; (C) *Ocellularia mordenii*; (D) *Borinquenotrema soredicarpum*; (E) *Porina americana*; (F) *Rhabdodiscus emersellus;* (G) *Wirthiotrema glaucopallens*; (H) *Coenogonium leprieurii**.

Plate 12

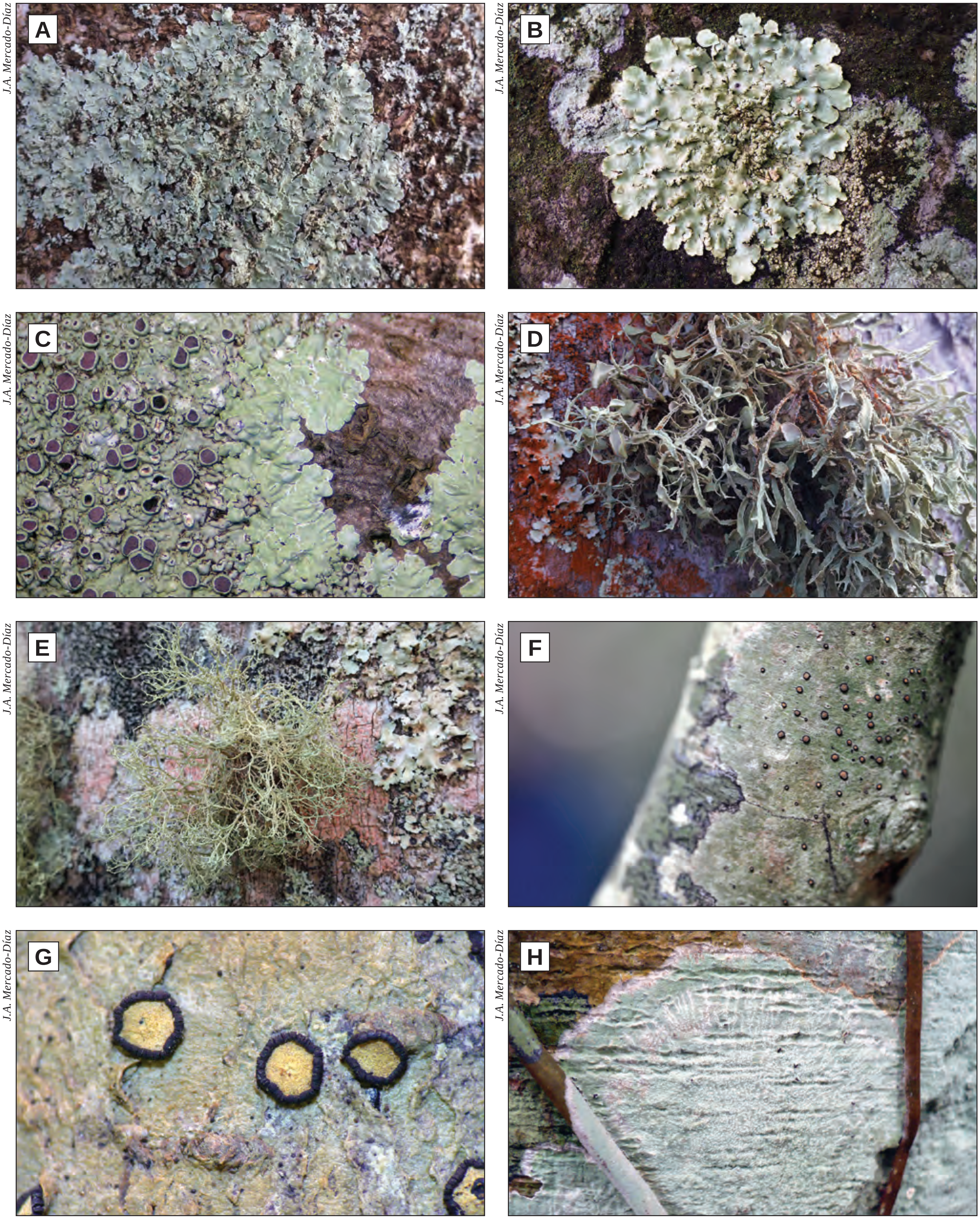

Plate 12—(A) *Physcia atrostriata**; (B) *Parmotrema praesorediosum**; (C) *Dirinaria purpurascens*; (D) *Ramalina complanata**; (E) *Ramalina peruviana**; (F) *Cresponea melanocheiloides**; (G) *Cresponea melanocheiloides* (detail); (H) *Cryptothecia striata**.

Plate 13

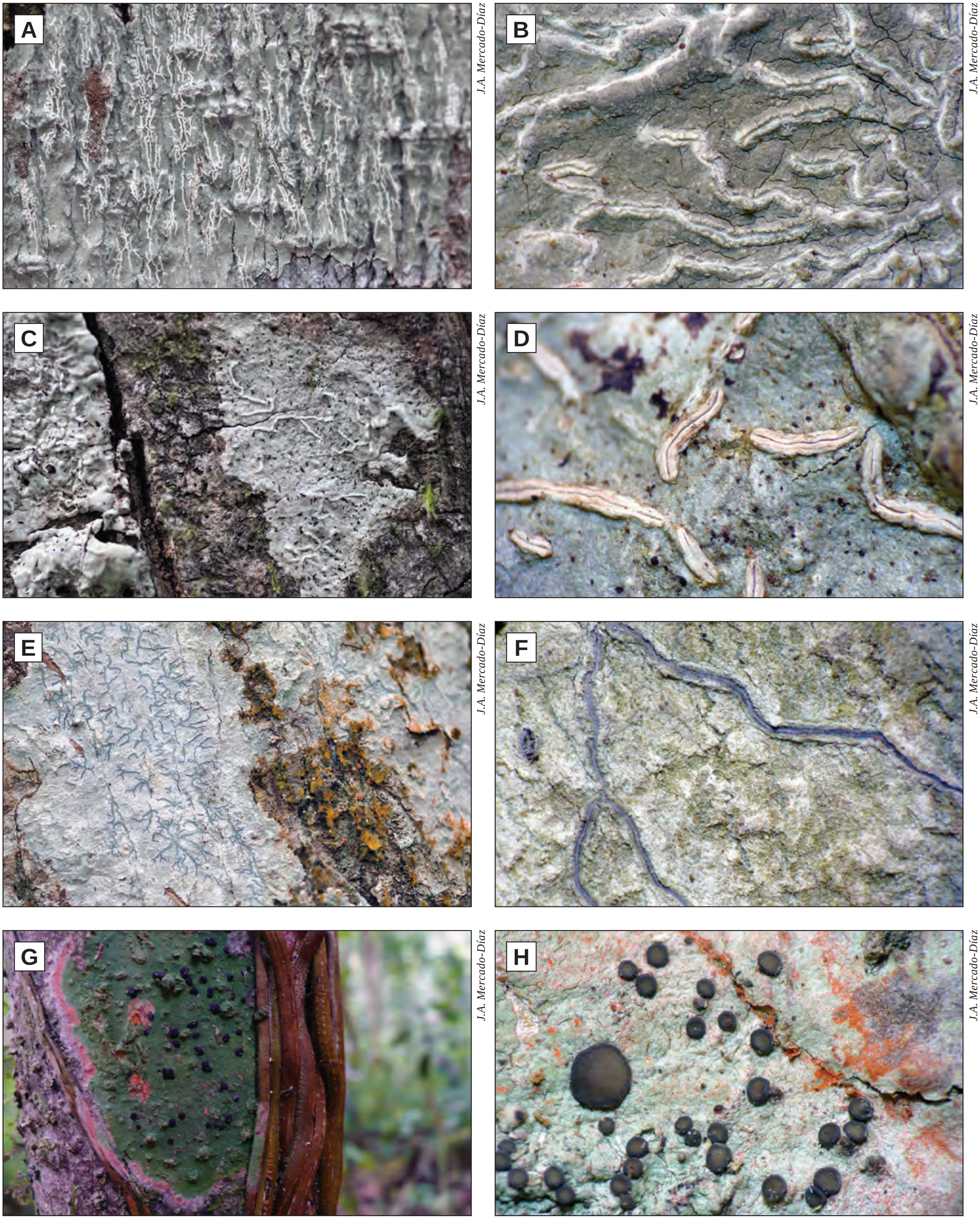

Plate 13—(A) *Diorygma poiteai**; (B) *Diorygma poiteai* (detail); (C) *Hemithecium balbisii**; (D) *Hemithecium balbisii* (detail); (E) *Graphis glaucescens**; (F) *Graphis glaucescens* (detail); (G) *Malmidea piperis**; (H) *Malmidea piperis* (detail).

Plate 14

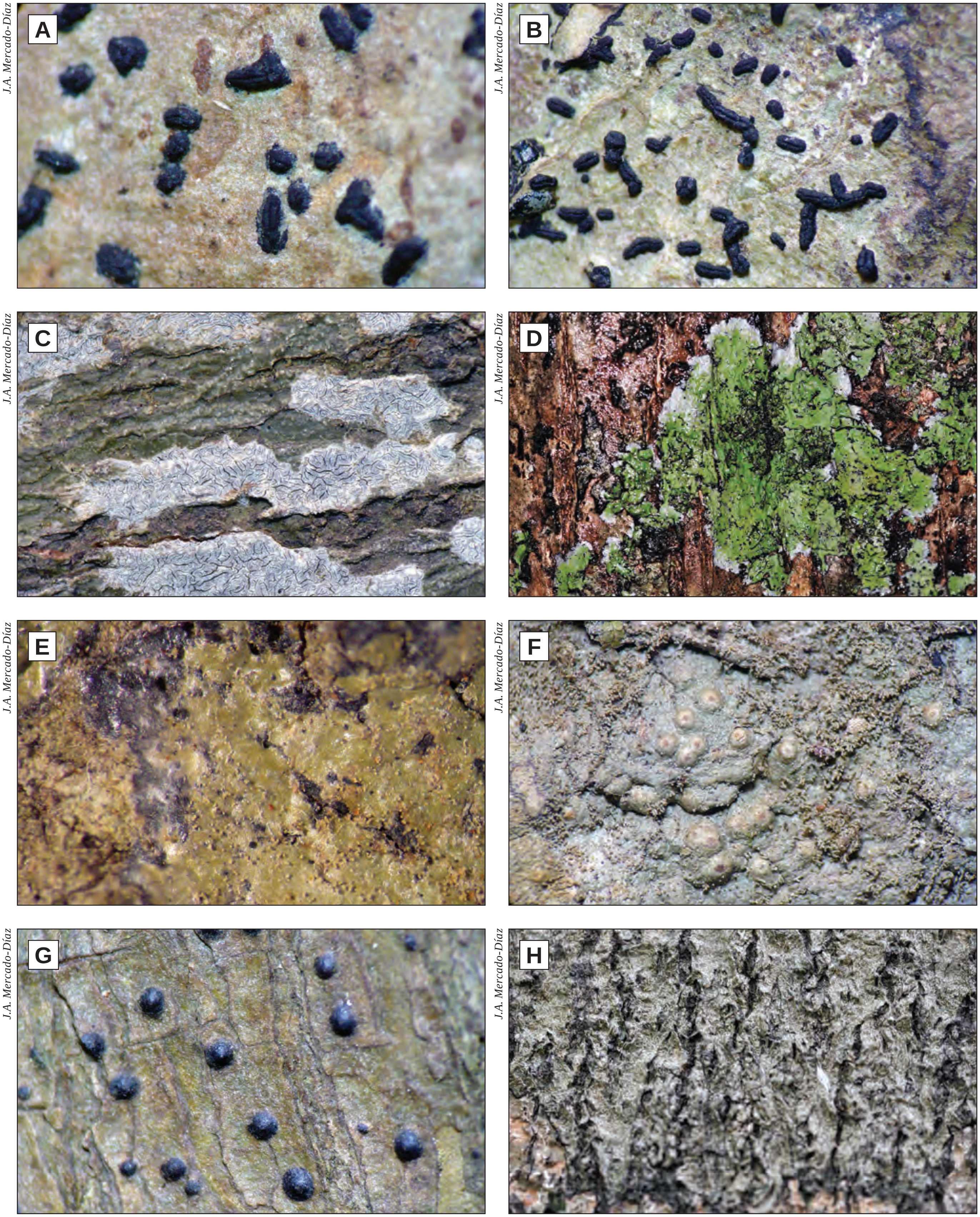

Plate 14—(A) *Opegrapha bonplandii*; (B) *Opegrapha dekeselii*; (C) *Phaeographis brasiliensis*; (D) *Porina distans**; (E) *Porina distans* (detail); (F) *Porina conspersa*; (G) *Pyrenula mamillana*; (H) *Fissurina subnitens* (between bark fissures)*.

Plate 15

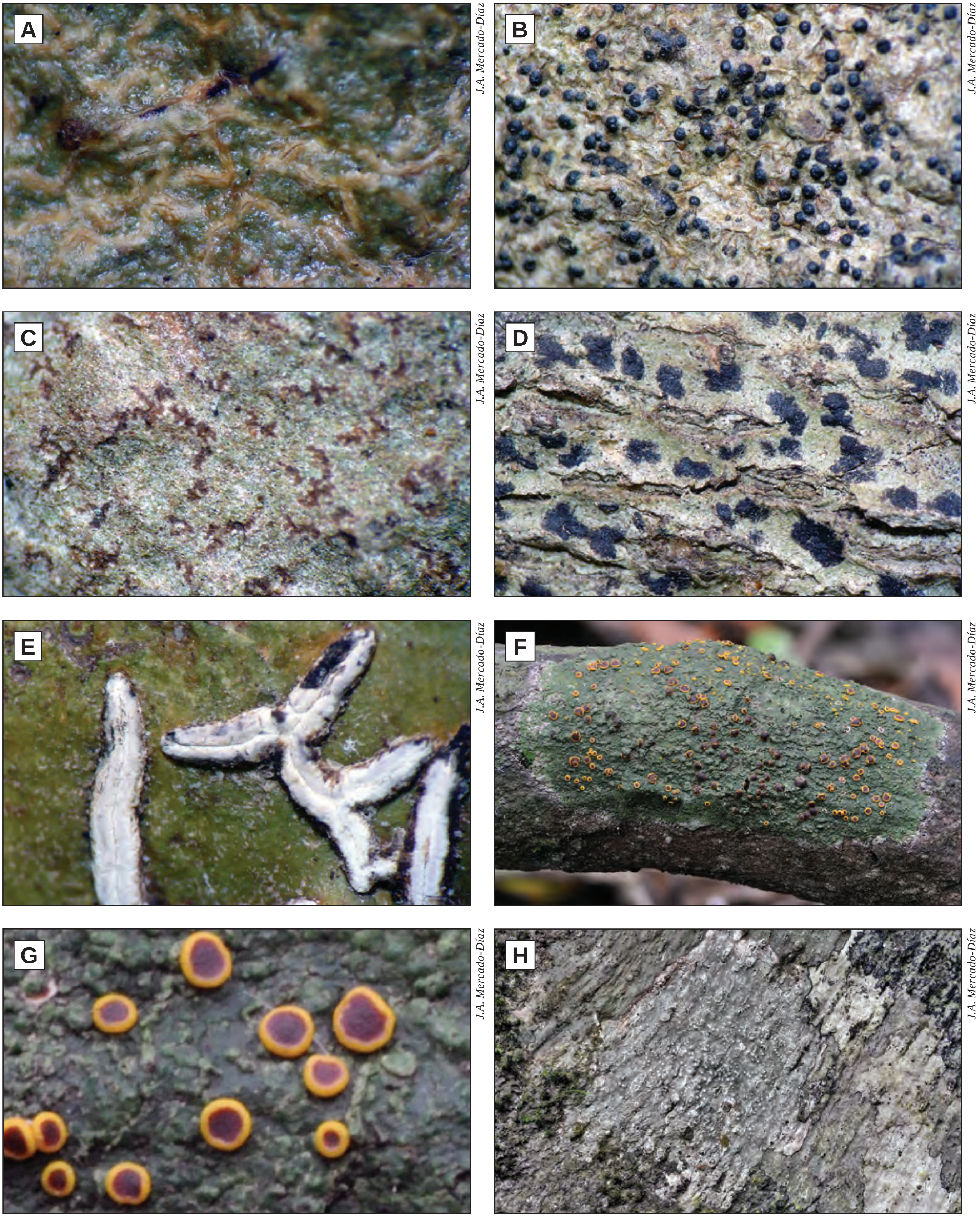

Plate 15—(A) *Fissurina subnitens* (detail); (B) *Anisomeridium subprostans*; (C) *Arthonia* aff. *pyrrholiza;* (D) *Arthonia bessalis*; (E) *Dyplolabia afzelii*; (F) *Letrouitia domingensis**; (G) *Letrouitia domingensis* (detail); (H) *Leucodecton bisporum**.

Plate 16

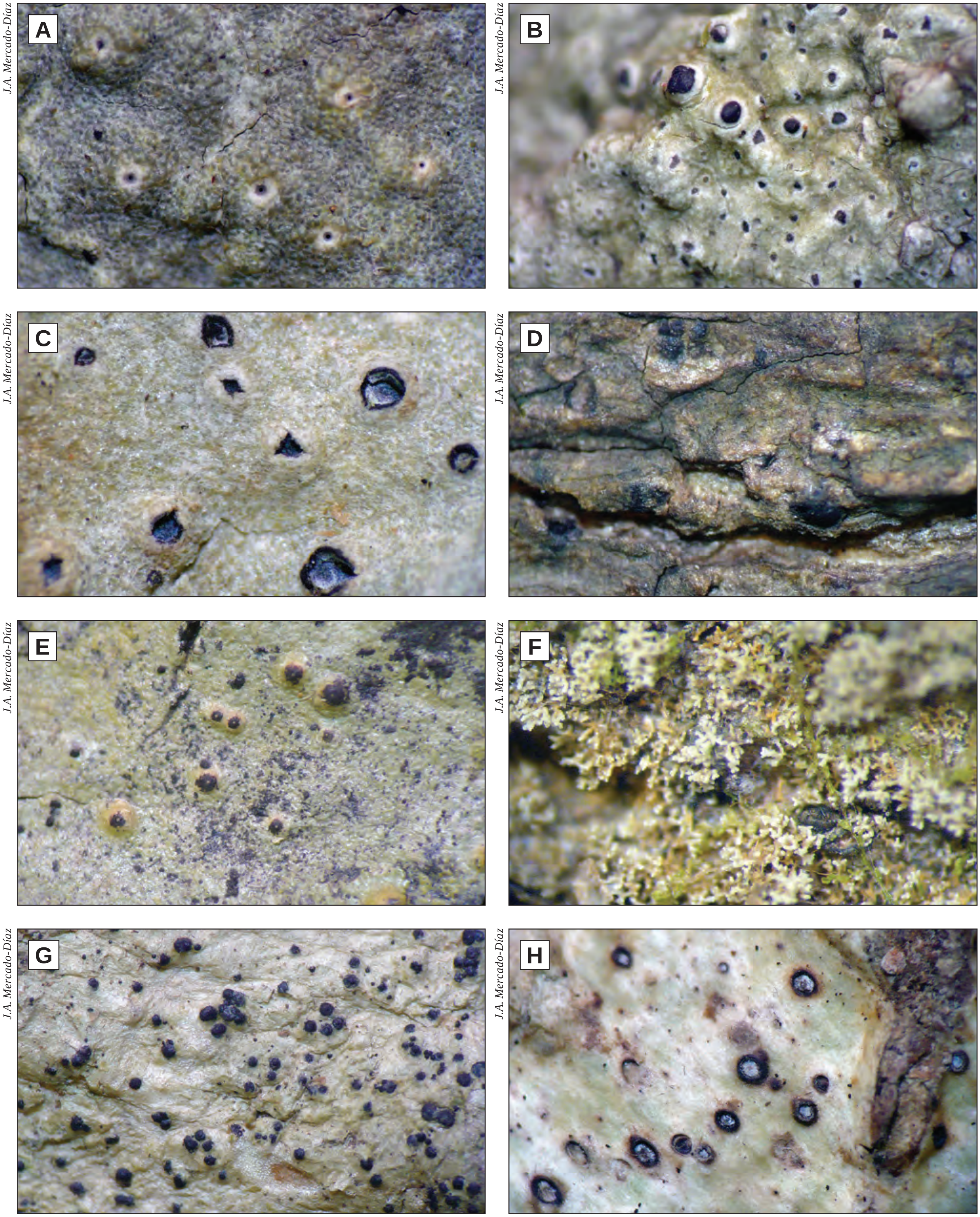

Plate 16—(A) *Leucodecton bisporum* (detail); (B) *Mazosia carnea*; (C) *Melanotrema platystomum*; (D) *Monoblastia borinquensis*; (E) *Porina tetracerae*; (F) *Psoroglaena cubensis*; (G) *Strigula phaea*; (H) *Trinathotrema stictideum*.

Plate 17

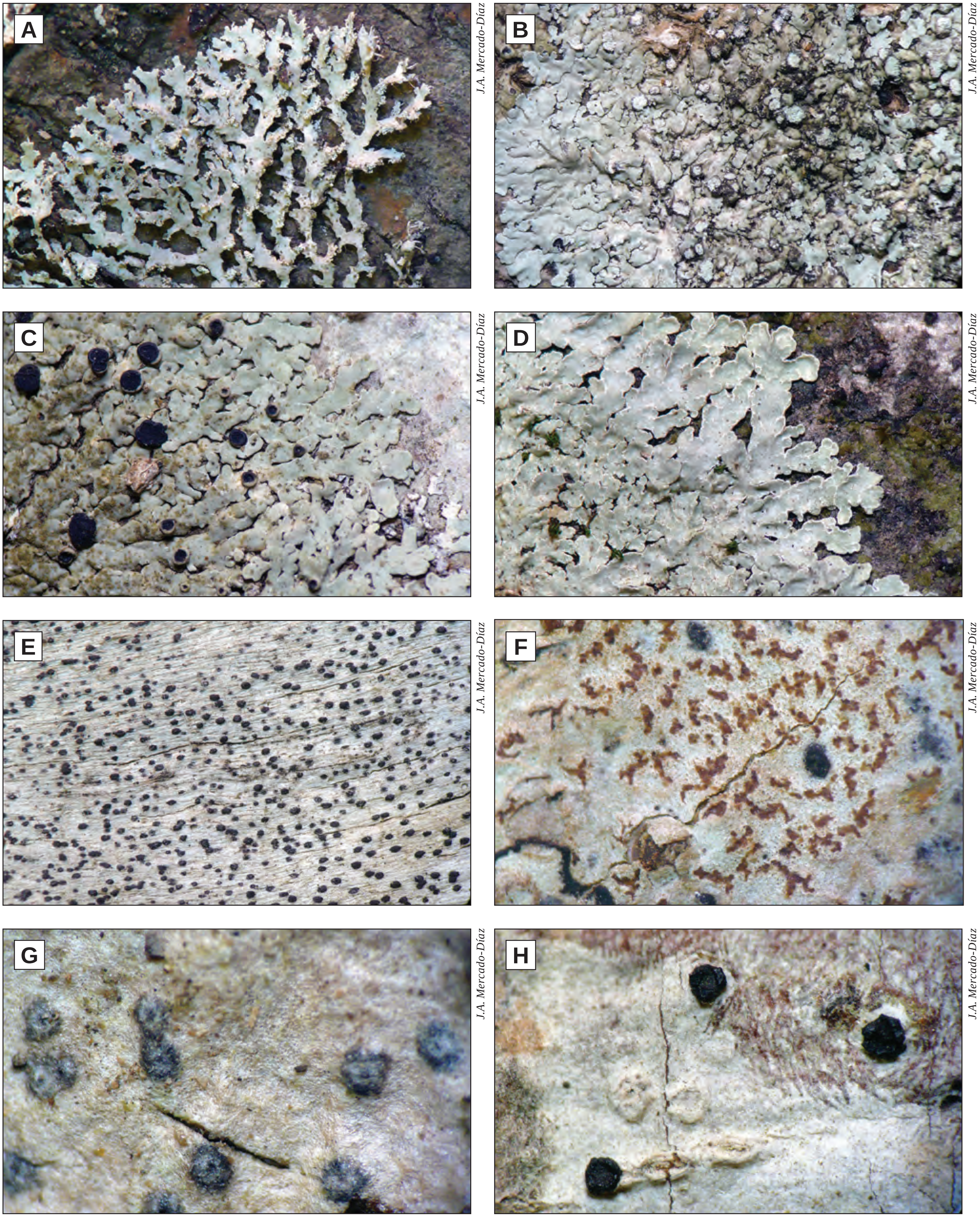

Plate 17—(A) *Physcia crispa*; (B) *Physcia sorediosa*; (C) *Pyxine berteriana*; (D) *Pyxine eschweileri*; (E) *Anisomeridium biforme*; (F) *Arthonia portoricensis*; (G) *Arthopyrenia majuscula*; (H) *Bactrospora denticulata*.

Plate 18

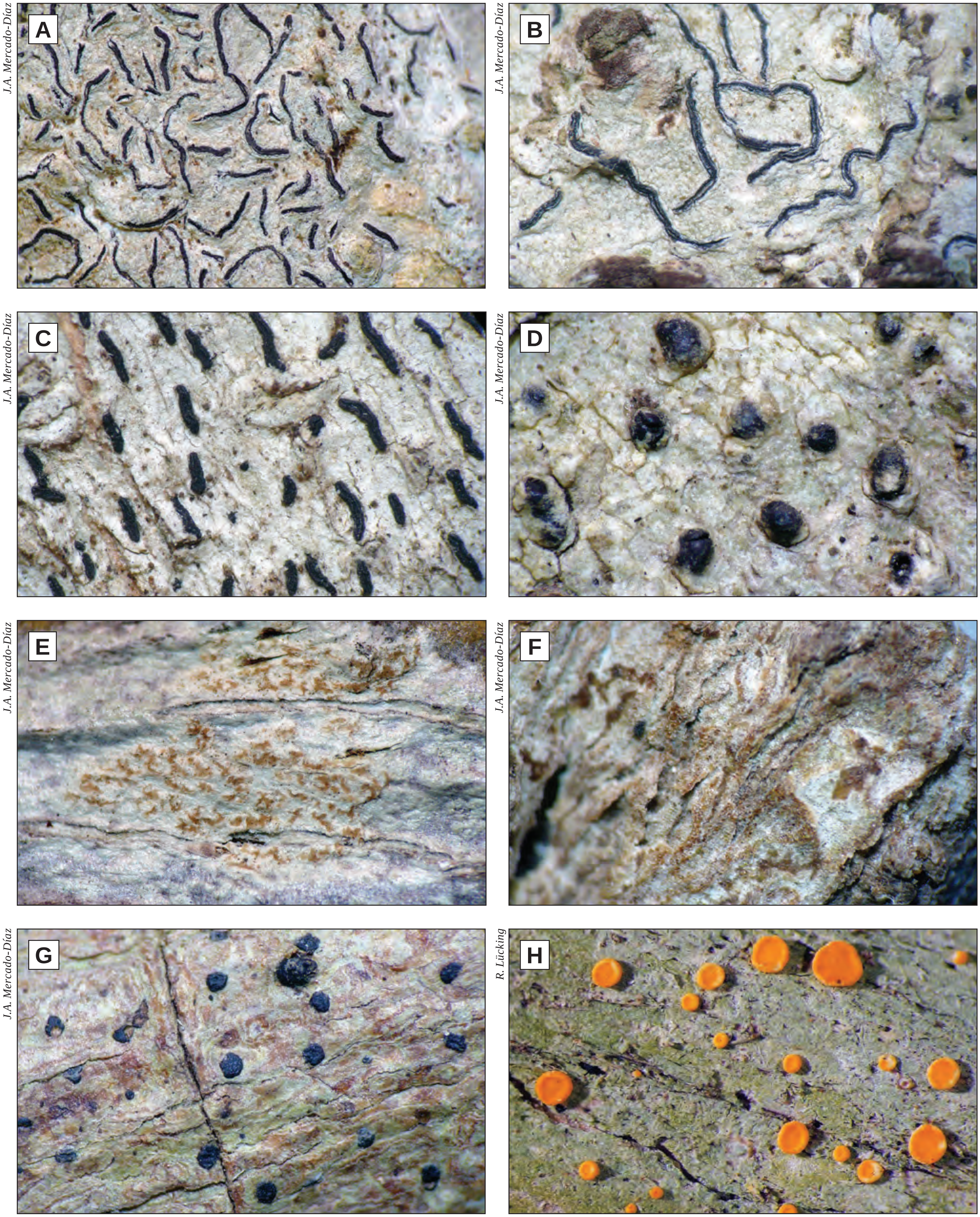

Plate 18—(A) *Graphis furcata*; (B) *Graphis tenella*; (C) *Opegrapha* cf. *varia*; (D) *Pyrenula quassiaecola*; (E) *Arthonia antillarum*; (F) *Arthonia caribaea*; (G) *Celothelium dominicanum*; (H) *Coenogonium aurantiacum*.

Plate 19

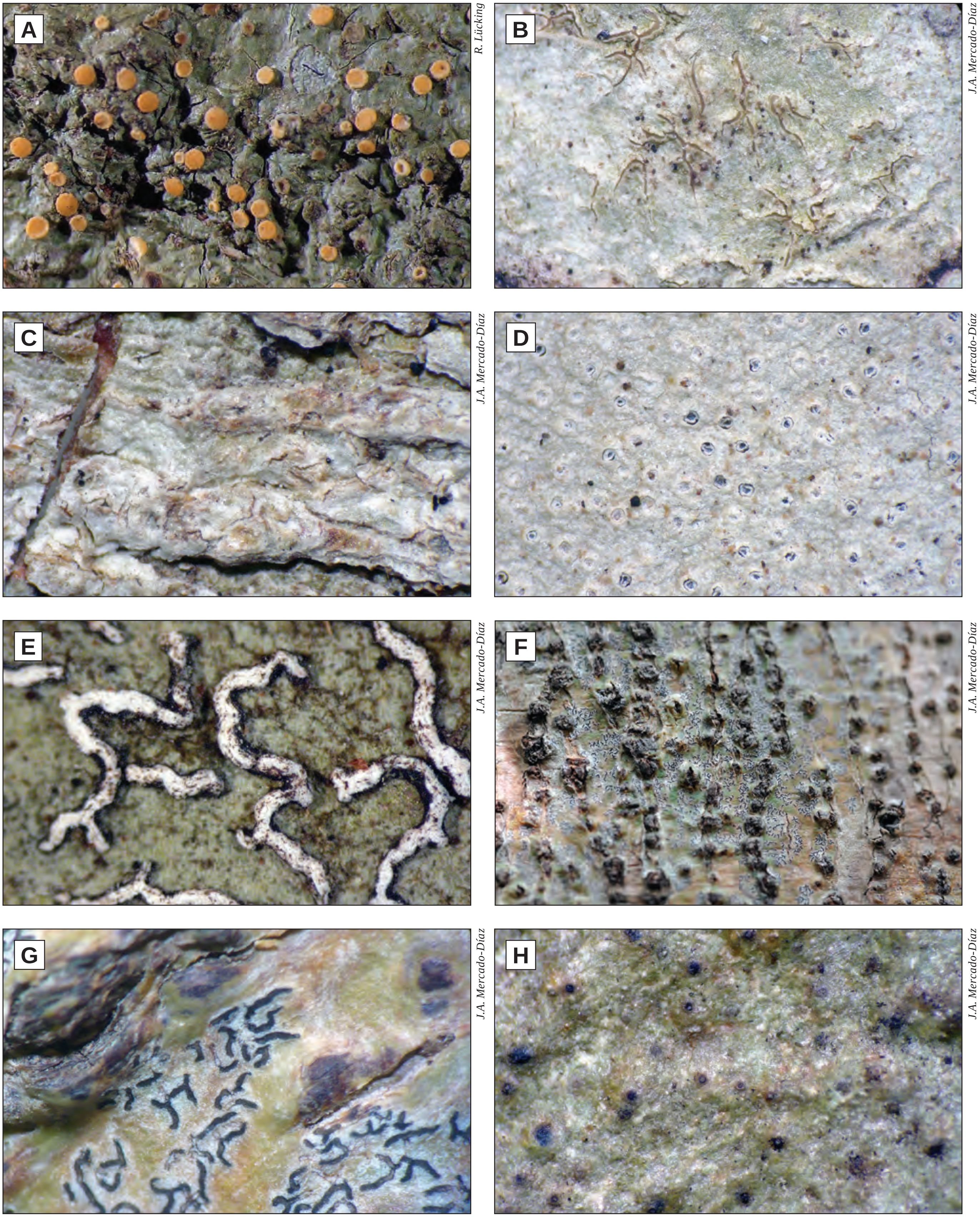

Plate 19—(A) *Coenogonium borinquense*; (B) *Enterographa multilocularis*; (C) *Fissurina tachygrapha*; (D) *Leucodecton occultum*; (E) *Opegrapha astraea*; (F) *Phaeographis inusta* (between lenticels); (G) *Phaeographis inusta* (detail); (H) *Pyrenula thelomorpha*.

Plate 20

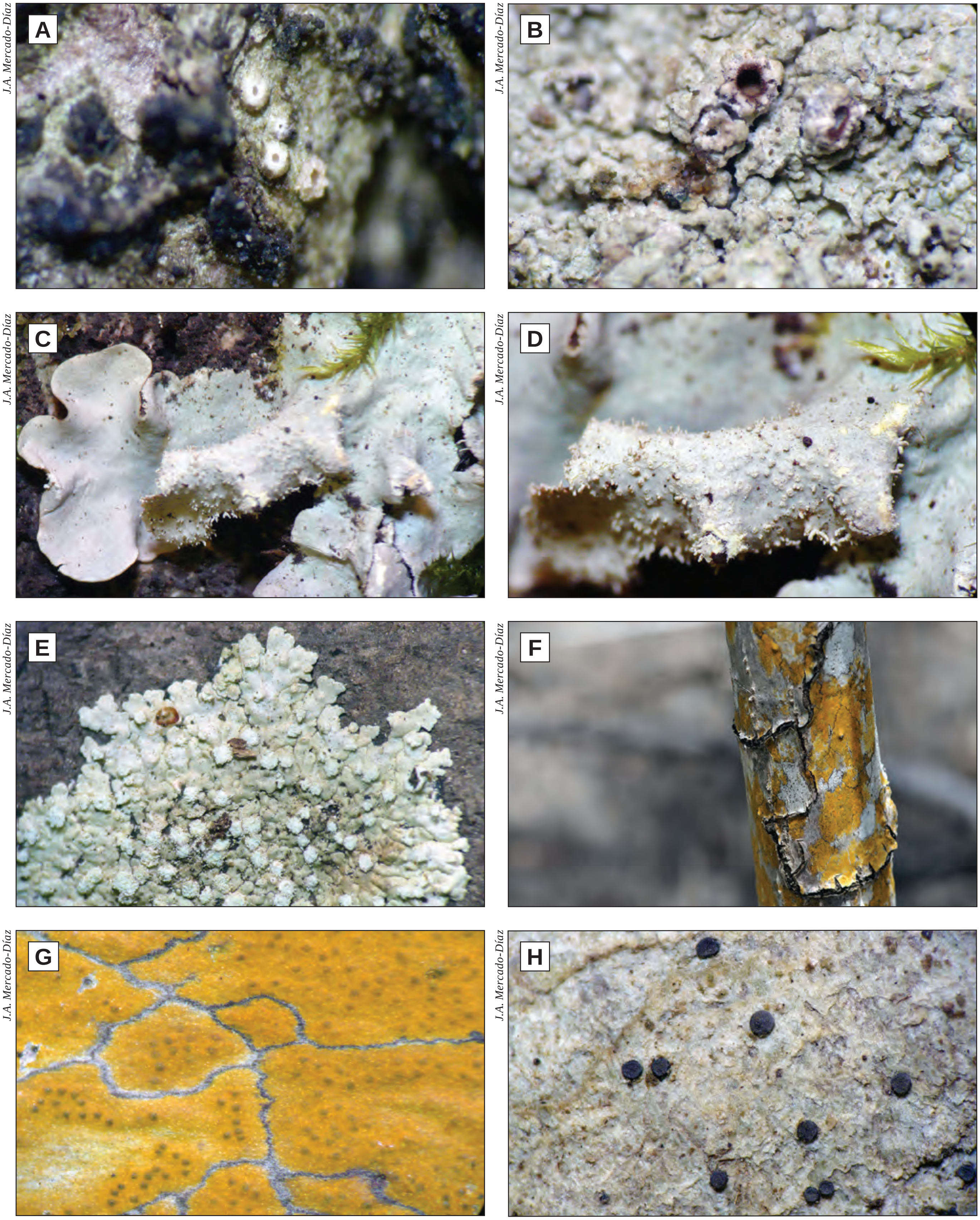

Plate 20—(A) *Ramonia rappii*; (B) *Ramonia valenzuelana;* (C) *Parmotrema endosulphureum*; (D) *Parmotrema endosulphureum* (isidia and yellow medulla); (E) *Physcia erumpens*; (F) *Pyrenula cerina**; (G) *Pyrenula cerina* (detail); (H) *Bactrospora myriadea*.

Plate 21

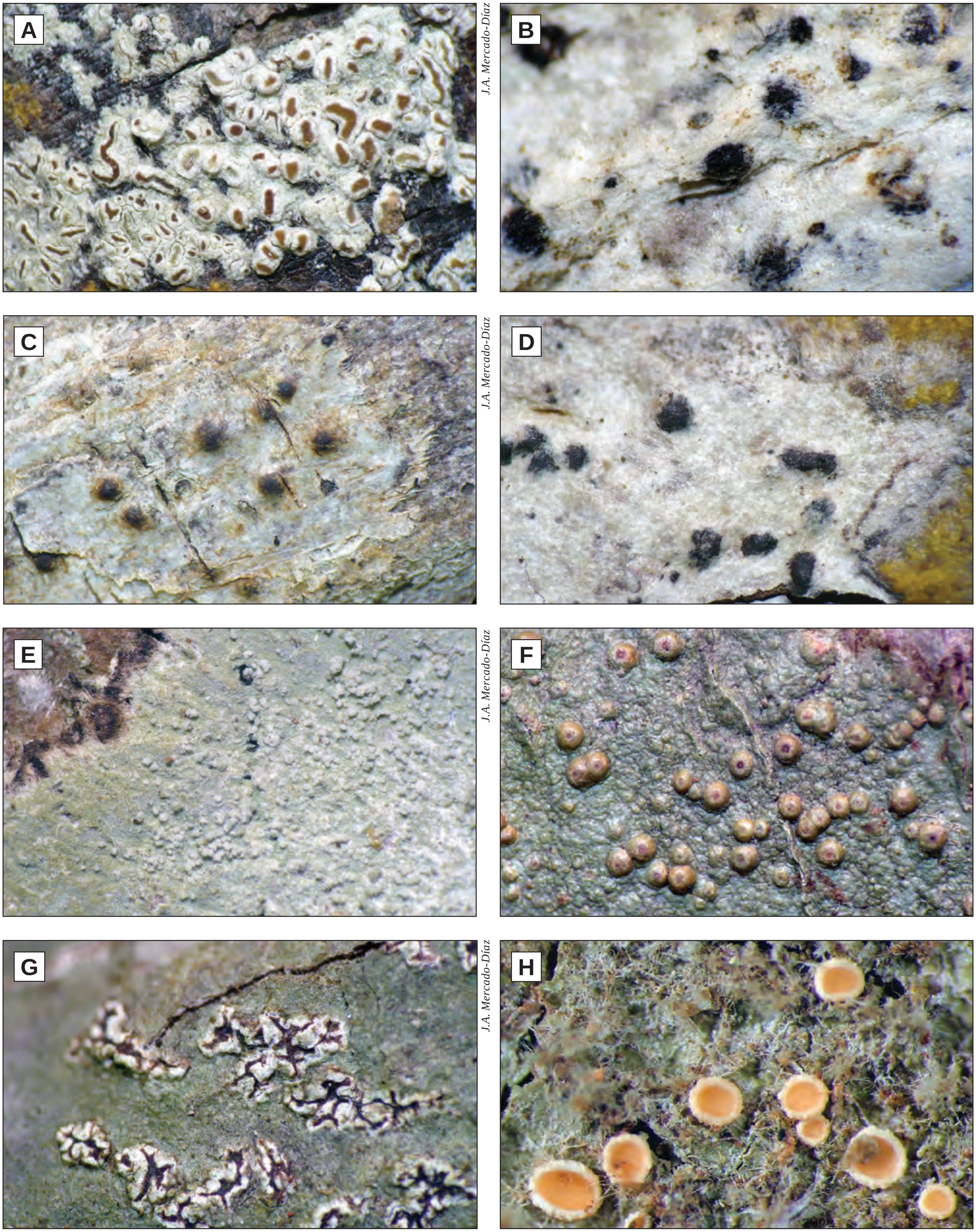

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Plate 21—(A) *Enterographa* aff. *anguinella*; (B) *Pyrenula cocoes;* (C) *Pyrenula ochraceoflava*; (D) *Pyrenula microcarpa*; (E) *Herpothallon minimum*; (F) *Porina curtula*; (G) *Arthonia* aff. *rubella*; (H) *Coenogonium dimorphicum.*

Plate 22

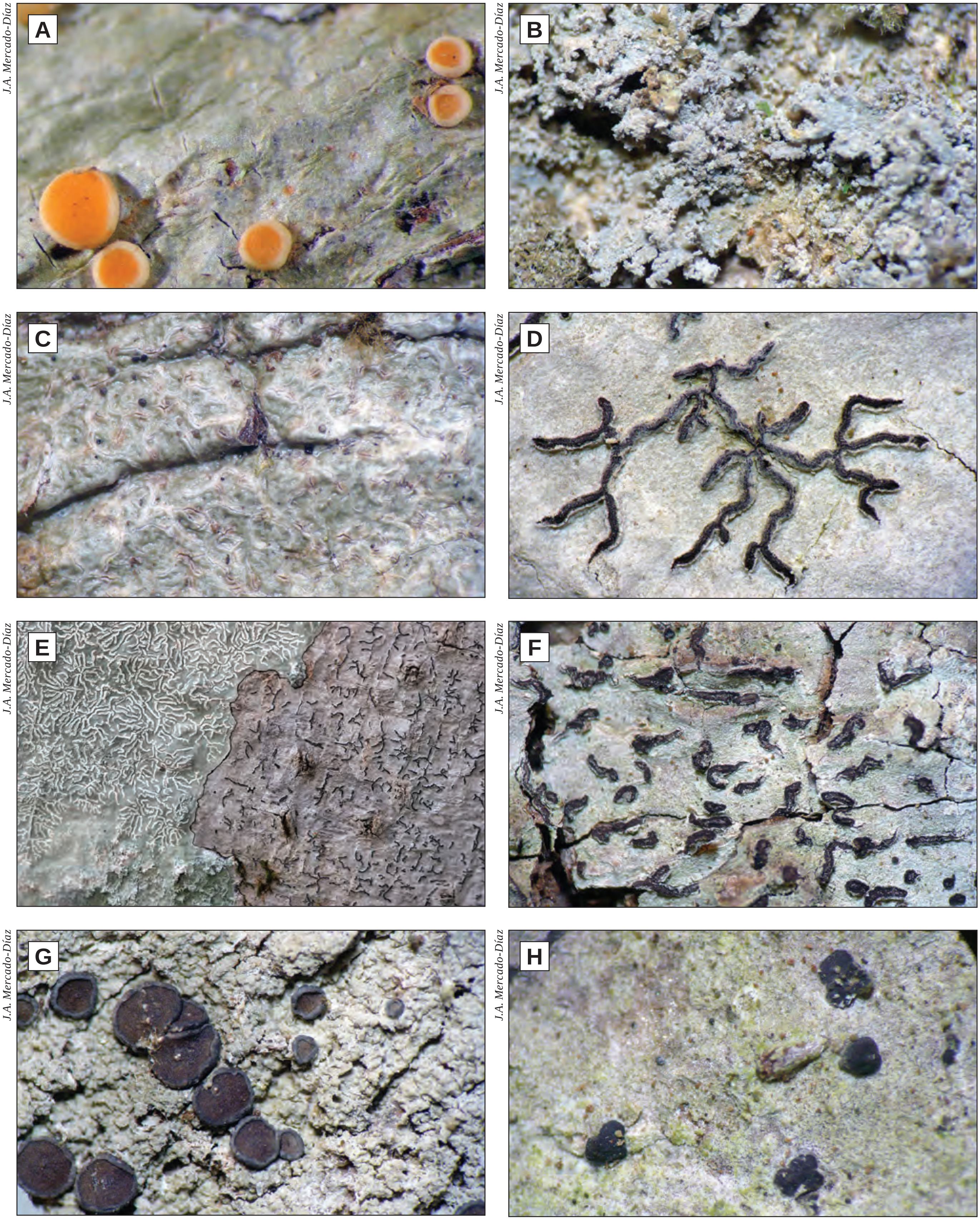

Plate 22—(A) *Coenogonium portoricense*; (B) *Crocynia gossypina;* (C) *Fissurina adscribens*; (D) *Graphis farinulenta*; (E) *Diorygma poiteai** (left) and *Graphis farinulenta** (right); (F) *Lecanographa lyncea*; (G) *Malmidea* aff. *coralliformis*; (H) *Schismatomma rappii*.

Lichen communities—

Along with the tabonuco and lowland moist forests (see below), palo colorado forests in El Yunque National Forest are perhaps one of the most lichen-diverse forest ecosystems of Puerto Rico. About 85 species have been found in sampled areas of this forest type. Sampled areas of palo colorado forests resulted in the highest number of species within the genera *Ocellularia*, *Chapsa*, *Malmidea*, *Phyllopsora*, *Rhabdodiscus*, and *Thelotrema*. Species of *Ampliotrema*, *Compositrema*, and *Paratopeliopsis* were found only in this forest type (Mercado-Díaz et al., in press). Palo colorado forests are second to elfin woodland forests in the number of species within the genus *Clandestinotrema*. This confirms that similar to other forests in the Neotropics, species within this genus are limited to high-elevation forests (Rivas-Plata et al. 2008).

Filamentous lichens are evident in palo colorado forests in El Yunque National Forest, where species like *Coenogonium linkii* (plate 2G) are occasionally found at the base of trees. Basidiolichens are also present in these forests, more commonly the species *Dictyonema sericeum* (plate 1B). Foliose and fruticose lichens are mostly absent under the shaded understory; only microfoliose species within the genus *Phyllopsora* may be observed. Several species with **byssoid** growth habit including *Herpothallon aurantiacoflavum* (plates 2H and 3A), *H. granulare* (plates 2H and 3B), and *Dichosporidium nigrocinctum* (plate 3, C and D) are frequently found in these forests.

Common corticolous species in the palo colorado forest include *Chapsa thallotrema* (plate 1, E and F), *Coenogonium linkii*, *Dichosporidium nigrocinctum*, *Dictyonema sericeum*, *Graphis rhizocola* (plate 3E), *Herpothallon aurantiacoflavum*, *Malmidea nigromarginata* (plate 3F), *Myeloconis guyanensis* (plate 3G), *Ocellularia praestans* (plates 3H and 4A), and *Porina nucula* (plate 4B). Many of these species can also be found in other ecosystem types in El Yunque National Forest.

Several corticolous lichens have been found only in sampled areas of palo colorado forests in El Yunque National Forest. Some of these include *Ampliotrema rimosum* (plate 4C), *Arthonia* spp. (yellow margin) (plate 4D), *Chapsa alborosella* (plate 4E), *Clandestinotrema* cf. *tenue* (plate 4F), *Coenogonium nepalense* (plate 4G), *Graphis dimidiata* (plate 4H), *Malmidea furfurosa* (plate 5A), *M. vinosa* (plate 5B), *Paratopeliopsis caraibica* (plate 5C), *Ocellularia* aff. *perforata* (plate 5D), *O. cavata* (plate 5E), *O. crocea* (plate 5F), *O. dolichotata* (plate 5G), *O. rhabdospora* (plate 5H), and *Platythecium grammitis* (plate 6A).

At least 11 morphotypes of thelotremoid lichens have been found in sampled areas of palo colorado forests in El Yunque National Forest (Rivas-Plata et al. 2008). These are the encountered morphotypes and several representative species:

Ampliotremoid: *Ampliotrema rimosum*
Chroodiscoid: *Chapsa alborosella*, *Astrochapsa platycarpella*
Leprocarpoid: *Chapsa dissuta*, *C. esslingeri*
Melanotremoid: *Clandestinotrema leucomelaenum*
Tenuitremoid: *Clandestinotrema* cf. *tenue*
Myriotremoid: *Paratopeliopsis caribica*
Ocellularioid: *Ocellularia crocea*, *O. perforata*, *O. tacarcunae*
Rhodostromoid: *Ocellularia cavata*, *O. rhodostroma*, *O. xanthostroma*
Praestantoid: *Ocellularia praestans*, *O. rhabdospora*, *O. dolichotata*
Stegoboloid: *Rhabdodiscus emersus*, *R. schizostomus*, *R. isidiiferus*
Thelotremoid: *Thelotrema porinoides*, *T. lepadodes*

Sierra Palm Forest

Environment—

In Puerto Rico, the sierra palm forest ecosystem (palm break) is found mostly within the lower montane wet forest life zone but might also reach areas classified as subtropical wet and subtropical rain forest (fig. 18). This forest type consists of nearly pure stands of *Prestoea acuminata* var. *montana* (Gould et al. 2006, Miller and Lugo 2009). Palm forest stands have a mean annual temperature of 20.7 °C and a mean annual precipitation of 3956 mm. These forests may cover nearly 11 percent


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Figure 18—The understory of a sierra palm forest in El Yunque National Forest, Puerto Rico.

of the Luquillo Mountains (Gould et al. 2006, Miller and Lugo 2009, Weaver 2012). Some of the characteristics of the "palm break" include its high dominance and a sharp ecotone with adjacent associations (Miller and Lugo 2009). The sierra palm forest is present in the 730 to 915 m altitudinal zone and can be found frequently interspersed with palo colorado and tabonuco forests in El Yunque National Forest (Miller and Lugo 2009).

Vegetation—
Plant communities of the sierra palm forest are mostly found in azonal, steeply sloping sites dominated by *P. acuminata* var. *montana* and are characterized by having a high abundance of epiphytes (Gould et al. 2006) (fig. 19). The development of an understory in the sierra palm forest is poor and occasionally absent. Soils are periodically covered by herbaceous vegetation and mosses (Lugo 2005). Five endemic tree species with diameter at breast height > 2 cm are commonly found in sierra palm forests in El Yunque National Forest, the most abundant being *Henriettea squamulosum* (Cogn.) W.S. Judd, *Eugenia borinquensis*, and *Cyathea arborea* (L.) Sm. (Gould et al. 2006). The abundance of *Cecropia schreberiana*


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Figure 19—Patches of the common crustose lichen *Chapsa thallotrema* in El Yunque National Forest, growing on the trunk of *Prestoea acuminata* var. *montana* in a sierra palm forest.

Miq. in the sierra palm forest is indicative of past hurricane disturbance (Gould et al. 2006). When occurring in the tabonuco forest, *P. acuminata* var. *montana* does not form any particular association in the forest canopy and is frequently found in the understory and in microenvironments that are water-saturated (Lugo 2005). See table 2 for common names of plant species.

Lichen communities—

Perhaps the most distinctive characteristic of the sierra palm forest in terms of its lichen flora is that it has the lowest species diversity compared to the rest of the forest types in El Yunque National Forest. Only 24 species have been found in sampled areas of this forest type. Despite its low species diversity, lichens in the sierra palm forest are usually more evident than in other forest types of El Yunque National Forest owing to the frequent occurrence of foliose lichens on tree trunks. For example, species in the genus *Sticta* (plate 6B) were mostly observed within this forest type. Many species of *Leptogium*, such as *L. azureum* (plate 6C) and *L. denticulatum* (plate 6D), are commonly found in the sierra palm forests. The new species *Thalloloma rubromarginatum* has been found only in this forest type (Mercado-Díaz et al., in press).

Most of the lichen flora in palm forests is crustose. *Coenogonium linkii* (plate 2G) is an example of filamentous species found in these forests. Byssoid growth forms are represented by species of *Herpothallon*, like *H. granulare* (plates 2H and 3B).

Some of the most commonly encountered lichen species of the sierra palm forest are *Chapsa thallotrema* (plate 1, E and F), *Coenogonium linkii*, *Graphis duplicata* (plate 6E), *Herpothallon granulare*, *Leptogium azureum*, *Porina subpungens* (plate 6F), and *Thelotrema porinoides* (plate 6G). Several of these species may also be found in other ecosystem types in El Yunque National Forest. Only a few species have been found exclusively in sampled areas of this forest type. Some of these include *Arthonia complanata* (plate 6H), *Graphis proserpens* (plate 7A), *Fissurina* sp. nov. (plate 7, B and C), *Megalotremis lateralis* (plate 7D), *Pyrenula* aff. *fetivica* (plate 7E), and *Sticta beauvoisii* (plate 7F).

Only two morphotypes of thelotremoid lichens have been found in sampled areas of sierra palm forests in El Yunque National Forest (Rivas-Plata et al. 2008). These are the encountered morphotypes and their representative species:

Sorediotremoid: *Chapsa thallotrema*
Thelotremoid: *Thelotrema porinoides*

It is interesting, from an ecological perspective, that most of the corticolous lichens occurring in sierra palm forests grow on the trunks of tree species other than *P. acuminata* var. *montana*, which is the dominant tree in this ecosystem. Nonetheless, specimens of *P. acuminata* var. *montana* present in other forest types of El Yunque National Forest apparently have higher species diversity on their trunks than specimens occurring in pure sierra palm forest stands (table 3). A possible explanation for this phenomenon is that trees with high species diversity surrounding *P. acuminata* var. *montana* individuals in these other forests are facilitating the immigration of species to neighboring *P. acuminata* var. *montana* trees.

Table 3—Lichens that grow on *Prestoea acuminata* var. *montana* trees in different forest types in El Yunque National Forest, Puerto Rico

Species	Elfin	Palo colorado	Sierra palm	Tabonuco
Chapsa thallotrema	X	X	X	X
Chapsa alborosella		X		
Dichosporidium nigrocinctum				X
Graphis duplicata			X	X
Herpothallon rubrocinctum				X
Mazosia ocellata				X
Ocellularia sp.		X		
Ocellularia sp. A				X
Porina scabrida				X
Pyrenula aspitea				X
Pyrenula sp. A				X
Sterile crustose			X	
Thelotrema porinoides				X
Total	1	3	3	10

Tabonuco Forest

Environment—

The tabonuco forest type occurs mainly in mid- to high-elevation areas of Puerto Rico and its elevational range spans from 15 to 550 m (Brown et al. 1983) (fig. 20). Nonetheless, in mountains like those in Tres Picachos State Forest in Jayuya, this forest may be found at 800 m (Lugo 2005). This ecosystem is characterized by having high tree-species diversity per unit area (Gould et al. 2006) and the presence of tall broadleaf evergreen hardwood trees that commonly exhibit buttressed trunks (Miller and Lugo 2009). It harbors a diverse epiphyte flora and many species of lianas. Many of the plants present in the tabonuco forest exhibit drip-tip leaves. It has a mean annual precipitation of 3060 mm per year and a mean annual temperature of 23 °C (Gould et al. 2006). Water deficits in the tabonuco forest are very small and soil moisture usually drops below field capacity (Miller and Lugo 2009).


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Figure 20—The trunk and sap of *Dacryodes excelsa* in El Yunque National Forest. This trunk is almost completely covered with a greenish crustose lichen.

Vegetation—

The tabonuco forest is a closed broad-leaved forest that gets its name from its dominant tree, *Dacryodes excelsa* Vahl (fig. 21). Forest patches of this ecosystem in El Yunque National Forest could harbor about 40 tree species and about 86 plant species (Gould et al. 2006). These forests form a complete canopy at about 20 m. Other prominent species are *Sloanea berteriana* Choisy ex DC, *Manilkara bidentata* (A. DC.) A. Chev, and *Tetragastris balsamifera* (Sw.) Oken (Gould et al. 2006, Lugo and Miller 2009). After disturbances, *Cecropia schreberiana* invades open areas and rapidly closes the canopy. This forest type includes several rare endemic species like *Cordia borinquensis* Urb., *Rondeletia portoricensis* Krug. & Urb., and *Byrsonima wadsworthii* Little (Gould et al. 2006). Along with the palo colorado forest, the tabonuco forest has the highest number of native plant species per unit area (Gould et al. 2006). Lugo (2005) reported that the tabonuco forest has high populations of "microscopic fungi" colonizing leaf surfaces in the canopy. Most of these microscopic fungi are possibly foliicolous lichens that have been observed growing along with liverworts on the leaves of these forests. See table 2 for common names of plant species.


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Figure 21—Mosaic of lichens growing on the lower trunk of a tree in a tabonuco forest. El Yunque National Forest, Puerto Rico.

Lichen communities—

Tabonuco forests have one of the richest lichen biota in Puerto Rico, with at least 76 corticolous species recorded in sampled areas of this forest type in El Yunque National Forest. Perhaps because *D. excelsa* is a dominant element in these forests, it appears to be the tree species with the highest number of lichen taxa on its bark. There are at least 27 known species growing on the lower trunk sections of *D. excelsa* (see list below). Although not as conspicuous as *D. excelsa*, tree individuals of *Prestoea acuminata* var. *montana* are often found with several lichen species such as *Dichosporidium nigrocinctum* (plate 3, C and D), *Porina scabrida* (plate 7G), *Graphis duplicata* (plate 6E), and *Mazosia endonigra* (plate 7H). These forests also possess the highest number of *Porina* and *Herpothallon* species for any forest type discussed in this report. Species of *Acanthotrema* and *Borinquenotrema* have only been found in this forest type (Mercado-Díaz et al., in press).

Lichens that grow on *D. excelsa* trees in El Yunque National Forest, Puerto Rico:

Acanthotrema alboisidiatum
Arthonia aff. *bessalis*
Bacidia sp. A
Chapsa thallotrema
Dichosporidium nigrocinctum
Herpothallon aurantiacoflavum
Herpothallon rubrocinctum
Leucodecton compunctelum
Mazosia sp. A
Mazosia sp. B
Mazosia sp. nov.
Myeloconis guyanensis
Myriotrema sp. B
Ocellularia cf. *praestans*
Ocellularia mordenii
Ocellularia sp. D (sorediate)
Ocellularia umbilicata
Opegrapha sp. A
Phyllopsora sp. A
Phyllopsora buettneri
Porina (sterile)
Porina conspersa
Pyrenula macrocarpa
Pyrenula mastophoroides
Pyrenula fetivica

With the exception of occasional foliose lichens in upper canopy layers, nearly all lichen taxa documented in these forests are crustose. Several species with byssoid growth habit are commonly found; e.g., *D. nigrocinctum*, *Herpothallon aurantiacoflavum* (plates 2H and 3A), *H. rubrocinctum* (plate 8A), and *H. granulare* (plates 2H and 3B). Squamulose species are represented by several species of *Phylopsora*, like *P. buettneri* (plate 8B), *P. corallina* (plate 8C), and the basidiolichen *Cyphellostereum* (plate 1C). Fruticose lichens are absent in the understory, although species of *Usnea* (plate 8D) can be found in light-exposed conditions. Dimorphic species, like those in the genus *Cladonia* (e.g. *Cladonia subradiata*, plate 8F) are expected to be found in open areas in these forests, growing directly on the soil or on other exposed substrates; however, these have not yet been encountered.

Common lichen species within this forest type include *Arthonia platygraphidea* (plate 8G), *Arthothelium distendens*, (plate 8H), *Chapsa thallotrema* (plate 2, E and F), *Ocellularia interposita* (plate 9A), *Mazosia endonigra* (plate 7H), *Pyrenula macrocarpa* (plate 9B), and *Pyrenula massariospora* (plate 9C). Some of these species may also be found in other ecosystem types in El Yunque National Forest and even in forests at lower elevations. Corticolous species of more exposed conditions or occurring in the canopy include *Thelotrema porinoides* (plate 6G) and *Heterodermia speciosa* (plate 9D). Several species have only been found in sampled areas of this forest type; for example: *Acanthotrema alboisidiatum* (plate 9E), *Arthonia* aff. *bessalis* (plate 9F), *Arthothelium* sp. nov. (plate 9G), *Pseudochapsa dilatata* (plate 9H), *Chapsa elabens* (plate 10A), *Eugeniella* sp. nov. (plate 10B), *Herpothallon* aff. *pustulata* (plate 10C), *Letrouitia vulpina* (plate 10D), *Leucodecton compuctellum* (plate 10E), *Malmidea amazonica* (plate 10F), *Mazosia verrucosa* (plate 10G), *Megalotremis infernalis* (plate 10H), *Ocellularia* aff. *cavata* (plate 11A), *O. ascidioidea* (plate 11B), *O. mordenii* (plate 11C), *Borinquenotrema soredicarpum* (plate 11D), *Porina americana* (plate 11E), *P. scabrida*, *Rhabdodiscus emersellus* (plate 11F), and *Wirthiotrema glaucopallens* (plate 11G).

Tabonuco forests have the second highest diversity of thelotremoid lichens documented in El Yunque National Forest (compared to palo colorado forests). In this respect, at least nine morphotypes of thelotremoid lichens have been found (Rivas-Plata et al. 2008). The most numerous genus of thelotremoid lichens in this forest is *Ocellularia* with 12 species. These are the encountered morphotypes and several representative species:

Leprocarpoid: *Pseudochapsa dilatata*
Sorediotremoid: *Chapsa thallotrema*
Leucodectonoid: *Leucodecton compunctellum*
Myriotremoid: *Myriotrema* sp. nov., *Wirthiotrema glaucopallens*
Ocellularioid: *Ocellularia ascidiodea*, *O. perforata*, *O. umbilicata*
Rhodostromoid: *Ocellularia mordenii*, *O.* aff. *cavata*
Praestantoid: *Ocellularia cf. praestans*, *O. interposita*
Stegoboloid: *Rhabdodiscus emersus*, *R. emersellus*
Thelotremoid: *Thelotrema porinoides*

Lowland Moist Forest

Environment—

The lowland moist forest occurs in the lowland subtropical moist Holdridge life zone (Ewel and Whitmore 1973) (fig. 22). It covers more area than any of the other life zones described by Ewel and Whitmore (1973). Mean annual rainfall in the lowland moist forest varies from 1000 to 2200 mm and mean annual temperature is about 27.5 °C (Gould et al. 2006, Miller and Lugo 2009). This forest type occurs in a variable elevation range, from sea level to 671 m (Ewel and Whitmore 1973). Throughout the world, lowland moist forests are among the most intensively used life zones (Ewel and Whitmore 1973). In Puerto Rico, most of these forests were deforested in the past mainly because their climatic conditions are favorable for agricultural activities (Miller and Lugo 2009). Other forest ecosystems, like *Pterocarpus* wetlands and mangrove swamps, could be classified as lowland moist forests; however, their unique biological and environmental characteristics justify a separate formal description (see further sections).

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Figure 22—A tree of *Spathodea campanulata*, a fast-growing species commonly observed in lowland moist forests in Puerto Rico.

Vegetation—

This forest is characterized by trees up to 20 m tall with rounded crowns (Miller and Lugo 2009) (fig. 23). Dominant canopy vegetation includes several tree species such as *Manilkara bidentata*, *Ocotea leucoxylon* (Sw.) De Laness. and *Hymenaea courbaril* L. (Gould et al. 2006). *Faramea occidentalis* (L.) A. Rich. and *Inga laurina*

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Figure 23—Trunk of a tree in lowland moist forest. To the right, two thalli of *Cryptothecia striata*. Río Piedras, Puerto Rico.

(Sw.) Willd. are common understory species (Gould et al. 2006). These forests also have the highest mean number of nonnative plant species per unit area (Gould et al. 2006). Epiphytes are common but rarely cover the surface of branches and trees entirely (Miller and Lugo 2009). Many of the woody species are deciduous during the dry season (Miller and Lugo 2009). Because most of this forest type was subjected to intensive human use in the past, it is extremely difficult to find natural undisturbed stands.

Lichen communities—
Although most lowland moist forests in Puerto Rico have been subject to intense human alteration, these areas may be among the forest ecosystems with the highest number of lichen species on the island. At least 86 species of corticolous lichens were identified in the understory of these forests. These forests also exhibit the highest number of lichen genera represented in a forest type (37). Because lowland moist forests occupy most of the island's surface area (59 percent) (Miller and Lugo 2009), and include other interesting vegetation associations occurring in serpentine- and limestone-derived soils not discussed in this report, lichen species richness of these forests should be higher than that reported here.

The lichen biota of lowland moist forests in Puerto Rico is almost completely dominated by crustose growth forms. Filamentous growth forms may occasionally be found on the base of trunks, particularly the species *Coenogonium leprieurii* (plate 11H) and *Coenogonium linkii* (plate 2G). Foliose growth forms are rarely found in the shaded understory of these forests; however, several species such as *Physcia*, *Pyxine*, and *Parmotrema* have been seen on fallen canopy branches, indicating their presence in upper canopy layers. *Physcia atrostriata* (plate 12A), *Parmotrema praesorediosum* (plate 12B), and *Dirinaria purpurasens* (plate 12C) are commonly observed foliose lichens in marginal areas of these forests. Fruticose lichens like the species *Ramalina complanata* (plate 12D) and *Ramalina peruviana* (plate 12E) are occasionally observed in open areas of these forests.

Compared to other forest ecosystems presented here, lowland moist forests may have the highest diversity of species in the genera *Fissurina* and *Opegrapha*. Commonly encountered species of these forests include *Cresponea melanocheiloides* (plate 12, F and G), *Cryptothecia striata* (plate 12H), *Diorygma poiteai* (plate 13, A and B), *Hemithecium balbisii* (plate 13, C and D), *Graphis glaucescens* (plate 13, E and F), *Malmidea piperis* (plate 13, G and H), *Opegrapha bonplandii* (plate 14A), *Opegrapha dekeselii* (plate 14B), *Phaeographis brasiliensis* (plate 14C), *Porina distans* (plate 14, D and E), *Porina conspersa* (plate 14F), *Pyrenula mamillana* (plate 14G), and *Fissurina subnitens* (plates 14H and 15A).

Species that were only found in these forests include *Anisomeridium subprostan*s (plate 15B), *Arthonia* aff. *pyrrholiza* (plate 15C), *Arthonia bessalis* (plate 15D), *Coenogonium leprieurii*, *Cresponea melanocheiloides*, *Dyplolabia afzelii* (plate 15E), *Letrouitia dominguensis* (plate 15, F and G), *Leucodecton bisporum* (plates 15H and 16A), *Mazosia carnea* (plate 16B), *Melanotrema platystomum* (plate 16C), *Monoblastia borinquensis* (plate 16D), *Porina tetracerae* (plate 16E), *Psoroglaena cubensis* (plate 16F), *Strigula phaea* (plate 16G), and *Trinathotrema stictideum* (plate 16H).

There are at least five morphotypes of thelotremoid lichens present in sampled areas of lowland moist forests. These are the encountered morphotypes and their representative species:

Leprocarpoid: *Chapsa defecta*
Sorediotremoid: *Chapsa thallotrema*
Leucodectonoid: *Leucodecton bisporum*
Melanotremoid: *Melanotrema platystomum*, *Trinathotrema stictideum*
Glaucophaenoid: *Myriotrema erodens*

Dry Forest

Environment—

Dry forests have the highest temperatures and lowest precipitation of all forest ecosystems in Puerto Rico and are found within the subtropical dry forest zone (Ewel and Whitmore 1973) (fig. 24). These forests cover vast areas in southwestern Puerto Rico, offshore islands like Mona, Culebra, Vieques, Caja de Muertos, Desecheo, and smaller areas to the east around the vicinity of Fajardo (Lugo 2005, Miller and Lugo 2009). Dry forests mostly occur along the coast and their elevation spans from sea level to about 200 m (Lugo 2005). Because mean annual rainfall ranges from 600 to 1100 mm, water scarcity is the predominant environmental condition in these forests (Lugo 2005, Miller and Lugo 2009). Dry forest air temperatures can be extremely variable during the day, occasionally reaching more than 30 °C (Lugo 2005). Most dry forests in Puerto Rico occur on calcareous substrates, and their mean annual temperature is about 25 °C (Lugo 2005). Noncalcareous dry forests cover a smaller area (about 1.2 percent of the island) and their mean annual temperature might be slightly higher than calcareous dry forests (27.5 °C) (Gould et al. 2006, Lugo 2005).

Vegetation—

Vegetation of dry forest areas visited for this project is typical of dry forests occurring in noncalcareous substrates (fig. 25). Commonly encountered tree species include *Bursera simaruba* (L.) Sarg., *Bourreria succulenta* Jacq., *Quadrella*


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Figure 24—The understory of a dry forest. Former Naval Station Roosevelt Roads, Ceiba, Puerto Rico.

cynophallophora (L.) Hutch., *Erythroxylum brevipes* DC., *Neea buxifolia* (Hook. f.) Heimerl, and *Eugenia biflora* (L.) DC. (Gould et al. 2006). Plant species diversity per unit area was the highest (99 species per 300 m^2) among several forest ecosystems (Gould et al. 2006). Evergreen species are predominant and there is low dominance of deciduous species compared to dry forests occurring on calcareous substrates (Lugo 2005). In calcareous dry forests, soils accumulate little water because of their rocky nature and shallowness, creating arid conditions for plant growth (Lugo 2005). In this respect, plants in noncalcareous dry forests exhibit less extreme xeromorphic traits than their counterparts in calcareous dry forests. Overall, vegetation of the island's dry forests tends to form a complete ground cover and is mostly semideciduous on most soils (Miller and Lugo 2009). See table 2 for common names of plant species.


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Figure 25—Trunk of a tree in a dry forest. Note the mosaic of crustose lichens in the trunk. Former Naval Station Roosevelt Roads, Ceiba, Puerto Rico.

Lichen communities—
A total of 77 species of corticolous lichens has been found in sampled areas of this forest ecosystem. This suggests that, compared to other lowland forest ecosystems, these forests are among the richest in terms of their corticolous lichen biota. Trees of dry forests in the southwestern portion of the island have also been seen to contain high lichen cover and diversity. Southwestern dry forests have slightly different vegetation composition owing in part to the calcareous nature of their substrate and are therefore expected to vary in terms of their lichen composition. Although dry forests on calcareous substrates were not sampled for this work, it is suspected that, if taken into consideration, dry forests as a whole may contain the highest species diversity for any lowland ecosystem of the island.

As in other forest ecosystems, dry forests are dominated by crustose growth forms. Several foliose species are occasionally found, such as *Physcia crispa* (plate 17A), *Physcia sorediosa* (plate 17B), *Physcia atrostriata* (plate 12A), *Pyxine berteriana* (plate 17C), *Pyxine eschweileri* (plate 17D), and *Parmotrema praesorediosum* (plate 12B). Although fruticose species were not found, species such as *Ramalina complanata* (plate 12D) have been observed in similar forests around the region. Many lichens found in these forests are whitish or brightly colored (yellow, orange, etc.). This is a common characteristic exhibited by lichens growing in dry environments with high light exposure (Brodo et al. 2001).

Dry forests were found to have the highest diversity of species in the genera *Arthonia*, *Bactrospora*, *Physcia*, and *Pyrenula*. *Ramonia* species were only found in these forests. Some of the most common corticolous lichens found in these forests are *Anisomeridium biforme* (plate 17E), *Arthonia portoricensis* (plate 17F), *Arthopyrenia majuscula* (plate 17G), *Bactrospora denticulata* (plate 17H), *Graphis furcata* (plate 18A), *Graphis tenella* (plate 18B), *Mazosia endonigra* (plate 7H), *Opegrapha* cf. *varia* (plate 18C), *Porina nucula* (plate 4B), *Pyrenula quassiaecola* (plate 18D), and *Arthonia antillarum* (plate 18E). Among the species that have only been found occurring in these forests are *Arthonia caribaea* (plate 18F), *Celothelium dominicanum* (plate 18G), *Coenogonium aurantiacum* (plate 18H), *Coenogonium borinquense* (plate 19A), *Enterographa multilocularis* (plate 19B), *Fissurina tachygrapha* (plate 19C), *Graphis tenella*, *Leucodecton occultum* (plate 19D), *Opegrapha astraea* (plate 19E), *Phaeographis inusta* (plate 19, F and G), *Pyrenula telomorpha* (plate 19H), *Ramonia rappi* (plate 20A), and *Ramonia valenzuelana* (plate 20B).

Only two morphotypes of thelotremoid lichens were found in sampled areas representative of dry forests. These are the encountered morphotypes and their representative species:

Leucodectonoid: *Leucodecton occultum*
Sorediotremoid: Sorediate crustose lichen, possibly *Chapsa*

Mangrove Forest

Environment—

Mangrove forests grow near sea water and are found at lowland elevations (<5 m) within the lowland subtropical dry and moist Holdridge life zones (Ewel and Whitmore 1973) (fig. 26). Mean annual temperature is 27.3 °C and mean annual precipitation is 1414 mm (Gould et al. 2006). Mangrove forests are often referred to as tidal “fringing forests” because they thrive in an ecotonal fringe along protected tropical coasts, lagoons, bays, and offshore islands (Miller and Lugo 2009). Because salt water can flow upstream from estuaries to rivers, mangroves may extend kilometers inland, as far as the presence of salt water occurs (Miller and Lugo 2009). By 1975, about half of the mangrove forests of Puerto Rico had been destroyed by agricultural activities and other human activities along the coast. In the last few years, there has been a net gain in mangrove coverage as a result of their protected status (Martinuzzi et al. 2009, Miller and Lugo 2009). Mangrove areas are the most extensive estuarine forested wetlands. The largest (Bosque de Pinoñes) is just east of San Juan in the municipalities of Carolina and Loíza (Miller and Lugo 2009).

Figure 26—View of the forest floor in a mangrove forest. Trees, saplings, and pneumatophores of *Avicennia germinans*. Ceiba, Puerto Rico.

Vegetation—

There are four common mangroves species typical to Puerto Rico and the Caribbean: *Rhizophora mangle* L., *Avicennia germinans* (L.) L., *Laguncularia racemosa* (L.) C.F. Gaertn., and *Conocarpus erectus* L. (fig. 27). These forests are typically found as *Rhizophora mangle*–dominated stands on coastal and estuarine fringes and in basins as pure or mixed stands of *A. germinans* and *L. racemosa* (Gould et al. 2006). When found in the subtropical moist forest life zone, mangroves appear to grow taller than in the subtropical dry life zone (Miller and Lugo 2009). Mangrove forests have the lowest plant species diversity per unit area as compared to other plant communities in Puerto Rico, although most of their flora is native (Gould et al. 2006). Mangrove is a general term that can refer to numerous families, genera, and species in totally different taxons (Miller and Lugo 2009). All plant species occurring in mangrove forests are salt-tolerant, or "halophytes." Mangroves provide a safe wildlife habitat both on land and around their prop roots in water, dampen the power of storm waves, and help stabilize land that normally would be eroded to the sea. See table 2 for common names of plant species.

Lichen communities—

In terms of their lichen composition, mangrove forests along the coastline are perhaps the most species-poor forest ecosystems of the island. Only 18 lichen species have been identified in sampled areas of these forests. However, if inland mangrove

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Figure 27—Several trunks of young mangrove trees. Orange color patches belong to *Pyrenula cerina*, a common crustose lichen found in these forests. Las Cabezas de San Juan Natural Reserve, Fajardo, Puerto Rico.

forest systems are included, species diversity increases substantially. For example, one mangrove stand in Sabana Seca Naval Station alone has about 30 corticolous lichen species. A possible explanation for the higher species diversity observed in inland mangrove forests is that these forests are often close to other species-rich forest ecosystems that may be actually serving as a source of new species to these mangrove forests. For instance, the mangrove stand in the Sabana Seca Naval Station is only several meters away from a *Pterocarpus* forest.

Similar to other forest ecosystems, species with a crustose growth habit dominate in these ecosystems. Foliose species such as *Parmotrema endosulphureum* (plate 20 C and D) and *Physcia erumpens* (plate 20E) are occasionaly found. Fruticose growth forms are rare or absent in the understory of these forests.

The most conspicuous lichen element in these forests is the ubiquitous presence of *Pyrenula cerina* (plate 20F), growing almost exclusively on the trunk and aereal roots of *R. mangle*. Other species associated with *P. cerina* and commonly found in these forests include *Arthonia antillarum* (plate 18E), *Arthonia portoricensis* (plate 17F), and *Bactrospora myriadea* (plate 20H). The species *Enterographa* aff. *anguinella* (plate 21A), *Pyrenula cocoes* (plate 21B), *Pyrenula ochraceoflava* (plate 21C), *Pyrenula cerina*, and *Pyrenula microcarpa* (plate 21D) are commonly observed and have only been found occurring in these forests. Species in the genus *Graphis* have also been observed in mangrove forests.

No thelotremoid lichens were found during fieldwork for this study. Only sorediotremoid morphotypes (Rivas-Plata et al. 2008) are expected to be found in some mangrove forests of Puerto Rico. Although mangrove forests are not treated in Rivas-Plata et al. (2008), if their methods were to be applied for estimating ecological continuity, it can be predicted that even old, undisturbed mangrove forests around the island would be classified as “anthropogenic vegetation.” These facts highlight the importance of identifying suitable bioindicators of ecological continuity for this type of forest.

Pterocarpus Forest

Environment—

Pterocarpus forests occur in relict patches within the lowland subtropical moist Holdridge life zone (Ewel and Whitmore 1973) (fig. 28). They are mostly found on undisturbed freshwater, seasonally flooded, noncalcareous alluvial substrates (Gould et al. 2006). *Pterocarpus* wetlands commonly occur along the coast, although a few populations are present along streams in northeastern Puerto Rico (Alvarez-López 1990). Compared to mangrove and dry forests, *Pterocarpus* forests have slightly lower temperatures (mean annual temperature = 26.4 °C) and higher precipitation (mean annual precipitation = 1685 mm) (Gould et al. 2006). These forests occur in the most heavily populated coastal plain and are subject to disturbance from changes in the hydrologic regime, particularly those related to urban development (Gould et al. 2006). *Pterocarpus* forests were likely much more extensive on coastal plains and along riparian corridors prior to deforestation for agricultural activities.

Vegetation—

Most *Pterocarpus* forests are considered palustrine forested swamps that usually have more than 40 percent of their area in tree cover (Miller and Lugo 2009) (fig. 29). It is typically a monoculture of the tree species *P. officinalis* Jacq., which occupies the overstory and the fern *Acrostichum aureum* L. in the understory. Like mangrove forests, *Pterocarpus* forests have low plant species diversity, but most of their flora is composed of native species (Gould et al. 2006). *Pterocarpus* trees may occasionally be found among mangrove trees as part of floodplain forests in riverine estuaries (Miller and Lugo 2009). Common lianas found here include

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Figure 28—Trunk and buttressed roots of a *Pterocarpus officinalis* tree. Sabana Seca Naval Station, Toa Baja, Puerto Rico.

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Figure 29—Patches of crustose lichens growing on young *Pterocarpus officinalis* trees. Sabana Seca Naval Station, Toa Baja, Puerto Rico.

Ipomoea triloba L., *Paullinia pinnata* L., and *Hippocratea volubilis* L. Freshwater *Pterocarpus* communities exhibit great canopy heights, with trees reaching more than 34 m (Gould et al. 2006). As a result of former agricultural activities and other coastal development, *Pterocarpus* forests have been reduced to only a few remnant stands. It is believed that in Puerto Rico these forests occupy no more than 5 percent of their original range, making them deserving of special protection status (Miller and Lugo 2009).

Lichen communities—
Pterocarpus forests are almost entirely a monoculture of *P. officinalis*; therefore, most of the corticolous lichens found in these forests grow on the trunk of this tree species. Compared to other forest ecosystems, corticolous lichen species richness is moderate, with about 59 species found in sampled areas of this forest type. Lichens of *Pterocarpus* forests share some similarities with the lichen flora of lowland moist forests, particularly at the genus level. This is not surprising, as both forest types are found within the lowland subtropical moist Holdridge life zone (see above).

With the exception of fruticose lichens, most lichen growth forms are represented in these forests. As other forests, crustose growth forms dominate; however, foliose lichens such as *Parmotrema praesorediosum* (plate 12B), *Physcia erumpens* (plate 20E), and *Physcia sorediosa* (plate 17B), as well as squamulose species in the genus *Phyllopsora* can be found occasionally. Species of filamentous lichens such as *Coenogonium linkii* (plate 2G) can be frequently found on the base of tree trunks. *Dichosporidium nigrocinctum* (plate 3, C and D), *Herpothallon aurantiacoflavum* (plates 2H and 3A), and *H. minimum* (plate 21E) are examples of byssoid growth forms found sporadically in these forests.

Species that are commonly observed in these forests include *Diorygma poiteai* (plate 13, A and B; plate 22E), *Graphis glaucescens* (plate 13, E and F), *Hemithecium balbisii* (plate 13, C and D), *Opegrapha dekeselii* (plate 14B), *Physcia sorediosa* (plate 17B), and *Porina curtula* (plate 21F). Several species have only been found in this type of forest, e.g., *Arthonia* aff. *rubella* (plate 21G), *Coenogonium dimorphicum* (plate 21H), *Coenogonium portoricense* (plate 22A), *Crocynia gossypina* (plate 22B), *Fissurina adscribens* (plate 22C), *Graphis farinulenta* (plate 22, D and E), *Herpothallon minimum*, *Lecanographa lyncea* (plate 22F), *Malmidea* aff. *coralliformis* (plate 22G), and *Schismatomma rappii* (plate 22H). *Pterocarpus* forests have the highest number of *Coenogonium* species recorded among all sampled ecosystems.

Only two morphotypes of thelotremoid lichens were found in sampled areas representative of *Pterocarpus* forests. These are the encountered morphotypes and their representative species:

Sorediotremoid: *Chapsa* (sorediate)
Leprocarpoid: *Chapsa dissuta*

Concluding Remarks

Results from this study suggest that tabonuco and palo colorado forests of El Yunque National Forest, as well as lowland moist forests, are the ecosystems with the highest lichen diversity in Puerto Rico. Along with these ecosystems, other forests on the island, such as the state forests of Maricao, Toro Negro, Tres Picachos, and Carite, are expected to harbor the vast majority of lichens. Dry forests are also species-rich and make a significant contribution to the island's lichen diversity. The least diverse forests of the island are most likely mangrove and elfin woodland forests and those in highly human-disturbed areas, such as forests in urban environments.

Some evidence appears to suggest that tabonuco, palo colorado, *Pterocarpus*, and dry forests are areas harboring a high number of lichen species that may be endemic. For instance, four species from *Pterocarpus* and dry forests mentioned in this report (*Coenogonium aurantiacum*, *C. borinquense*, *C. dimorphicum*, and *C. portoricense*) appear to be endemic (Mercado-Díaz et al. 2013). Several new species from tabonuco, palo colorado, and sierra palm forests have been recently described and are potentially endemic taxa (Mercado-Díaz et al., in press).

Table 4 summarizes the number of species, genera, and families of corticolous lichens found in sampled areas of each forest type described in this report. In this sense, these values should be regarded as relative measures of species richness; they do not represent the total number of species found in these ecosystems. Although limitations related to our sampling approach and other external factors may have influenced the robustness of our estimates, we still consider this information valuable because it presents a rough idea of the diversity to be found in these forests. An example of how limitations related to sampling may have limited our estimates comes from the mangrove ecosystem. Namely, one of the mangrove forest plots was considerably higher in species richness than the two other mangrove forest plots sampled. It is thought that this higher-than-expected richness is associated with its proximity to an adjacent *Pterocarpus* forest fragment. If this plot were excluded, mangrove forests would total 17 species, 9 genera, and 7 families, less than half of the richness reported for all taxonomic levels presented for mangrove forests in table 4.

Table 4—Number of species, genera, and families of corticolous lichens occurring in sampled areas of each forest type described in this study

	Elfin woodland	Palo colorado	Sierra palm	Tabonuco	Dry	Lowland moist	Mangrove	*Pterocarpus*
Species	33	85	24	76	77	86	48	59
Genera	17	30	15	32	30	37	27	27
Families	8	15	10	14	17	17	18	14

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English Equivalents

When you have:	Multiply by:	To get:
Millimeters (mm)	0.0394	Inches
Meters (m)	3.28	Feet
Kilometers (km)	621	Miles
Hectares (ha)	2.47	Acres
Square kilometers (km^2)	.386	Square miles
Degrees Celsius (°C)	1.8 °C + 32	Degrees Fahrenheit

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Glossary

Apothecia—Disk or cup-like ascoma of Ascomycota.

Ascocarp—An anatomically differentiated structure of asci (sac-like, spore-bearing structure) and interascal hyphae enclosed within distinct layers of hyphae.

Ascomata—Fruiting bodies of Ascomycota.

Basidiolichen—Lichenized members of the Basidiomycota.

Basidiomata—Fruiting bodies of Basidiomycota.

Bioindicator—Species that can be used to monitor the health of an environment or ecosystem.

Byssoid—Entirely composed of delicate, densely interwoven threads.

Cilia—Long-acute, multicellular hair-like outgrowths with the appearance of an “eye lash,” generally originating from the margin or upper surface (but close to the margin) of a thallus lobe or along the margin of apothecia.

Columella—A sterile central axis within a mature ascocarp.

Corticolous—Inhabiting the bark of trees or shrubs.

Cyphellae—Pores recessed into the lower thallus surface, surrounded by a pale ring and lined throughout with loosely interwoven, non-gelatinized hyphae, originating from the medulla.

Crustose—General growth form where the entire thallus forms a crust.

Dimorphic—Having two growth forms.

Endolichenic—Living in close association with algal and fungal components inside a lichen thalli.

Epiphytes—A plant or plant-like organism growing on another plant

Epiphytic—Growing on plants or plant like organisms, as an epiphyte.

Exciple—An anatomical term generally referring to any lateral layer surrounding, embracing or enveloping an ascocarp.

Filamentous—Hair- or thread-like.

Foliicolous—Growing on the surface of leaves of vascular plants

Foliose—General growth form of a "leaf-like" thallus.

Fruticose—General growth form where the thallus is three-dimensional, either erect, pendulous (= pendent) or prostrate.

Gelatinous—Jelly-like, gel-like, with a consistency of a gel.

Isidia—A small (mostly 0.5 to 1 mm) asexual outgrowth of the thallus containing both mycobiont and photobiont. Often with a granular, warty, pin- or finger-shaped appearance.

Lichenization—Any complex organism composed of a fungus in symbiotic union with an alga.

Lobule (pl. Lobules)—A small (possibly juvenile) lobe; flattened and usually corticate on both the upper and lower side.

Morphotype—An informal group of taxa with similar or identical morphology.

Parasitism—A close association of organisms that is detrimental for one of the symbionts.

Pendulous—Type of fruticose growth which is much stouter, not as finely divided, and with vine-like branching pattern.

Photosymbiodeme—A lichen fungus forming morphologically and anatomically identical (isomorphic) or different (heteromorphic) thalli with different photobionts.

Pyrenocarp—A globose to flask-shaped ascocarp opening with a pore.

Pyrenocarpous—With a structure and appearance similar to a pyrenocarp.

Rhizines—Root-like strands of closely agglutinated hyphae on the lower side of a foliose thallus, usually thread-like to intricately branched, scant to more or less numerous; attaching a foliose thallus to its substrate.

Soredia (pl. Soralia)—Microscopic groups of photobiont cells aggregated by loosely interwoven hyphae, erupting from cracks or pores in the thallus surface with a finely powdery to coarsely granular appearance.

Schizidium (pl. Schizidia)—A scaly propagule, formed by flaking off from the thallus surface.

Squamule—A small, more or less complanate, scale-like thallus or thallus segment.

Squamulose—Forming squamules, referring to a growth form intermediate between crustose and foliose thalli.

Symbiosis—Any form of cohabitation where two organisms form a close association, thus living together either to the benefit (mutualism) or detriment of one another (parasitism) or without any apparent effect (commensalism).

Thallus (pl. Thalli)—The vegetative and assimilative body of both myco- and photobiont.

Thelotremoid—Typically referring to a fruit wart commonly observed in species of thelotremoid Graphidaceae where the thalline exciple and proper exciple are not adherent.