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A first assessment of the Ticolichen biodiversity inventory in Costa Rica and adjacent areas: the thelotremoid Graphidaceae (Ascomycota: Ostropales)

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Abstract

In a continuation of our biotic inventory of lichenized fungi in Costa Rica and adjacent areas, we present a treatment of the thelotremoid Graphidaceae, that is the genera and species formerly included in Thelotremataceae. A total of 186 species in 23 genera are reported for Costa Rica, plus an additional 30 taxa for adjacent areas (El Salvador, Nicaragua, Panama) that are expected to occur in Costa Rica. This is the highest number of thelotremoid Graphidaceae reported for any country in the world thus far, followed by Australia (173 species), Sri Lanka (130 species), and Panama (110 species). Together with our previous treatment of the genus *Graphis*, a total of 293 species of Graphidaceae have now been reported for Costa Rica in revised monographic works, with revisions of larger genera such as *Phaeographis* still pending, suggesting that the total number of Graphidaceae in Costa Rica is over 400. In the present monograph, the following genus and 40 species taxa are described as new to science: *Enigmotrema* Lücking *gen. nov.*, *Acanthotrema bicellularis* Sipman & Lücking, *spec. nov.*, *A. kalbii* Lücking, *spec. nov.*, *Chapsa defecta* Lücking, *spec. nov.*, *C. defectosorediata* Lücking, *spec. nov.*, *C. farinosa* Lücking & Sipman, *spec. nov.*, *C. perdissuta* Sipman & Lücking, *spec. nov.*, *C. sublilacina var. cyanea* Lücking, *spec. nov.*, *C. thallotrema* Lücking & N. Salazar, *spec. nov.*, *Clandestinotrema analorenae* Lücking, *spec. nov.*, *Enigmotrema rubrum* Lücking, *spec. nov.*, *Gyrotrema aurantiacum* Sipman, Lücking & Chaves, *spec. nov.*, *G. papillatum* Lücking, *spec. nov.*, *Leucodecton album* Sipman & Lücking, *spec. nov.*, *Myriotrema*

aggregans Sipman & Lücking, *spec. nov.*, *M. clandestinoides* Sipman & Lücking, *spec. nov.*, *M. classicum* Lücking, *spec. nov.*, *M. endoflavescens* Hale ex Lücking, *spec. nov.*, *M. frondosolucens* Lücking & Aptroot, *spec. nov.*, *Ocellularia albobullata* Lücking, Sipman & Grube, *spec. nov.*, *O. cocosensis* Lücking & Chaves, *spec. nov.*, *O. flavoperforata* Lücking, *spec. nov.*, *O. gerardii* Sipman, *spec. nov.*, *O. globifera* Kalb & Lücking, *spec. nov.*, *O. inspersata* Kalb & Lücking, *spec. nov.*, *O. inspersula* Lücking & Aptroot, *spec. nov.*, *O. isohypocrellina* Lücking & Kalb, *spec. nov.*, *O. laevigatula* Kalb & Lücking, *spec. nov.*, *O. laeviusculoides* Sipman & Lücking, *spec. nov.*, *O. praestantoides* Sipman, *spec. nov.*, *O. pseudopyrenuloides* Lücking, *spec. nov.*, *O. psorbarroensis* Sipman, *spec. nov.*, *O. subcarassensis* Sipman & Lücking, *spec. nov.*, *O. subpyrenuloides* Lücking, *spec. nov.*, *O. supergracilis* Kalb & Lücking, *spec. nov.*, *O. terrabensis* Kalb & Lücking, *spec. nov.*, *O. zamorana* Sipman, Lücking & Chaves, *spec. nov.*, *Thelotrema gomezianum* Lücking, *spec. nov.*, *T. submyriocarpum* Lücking, *spec. nov.*, *T. wilsonii* Sipman & Lücking, *spec. nov.*, and *Wirthiotrema duplomarginatum* Lücking, Mangold & Lumbsch, *spec. nov.* In addition, the following 19 new combinations are proposed: *Ampliotrema dactylizum* (Hale) Sipman, Lücking & Grube, *comb. nov.* [bas.: *Ocellularia dactyliza* Hale], *A. panamense* (Hale) Sipman & Lücking, *comb. nov.* [bas.: *Leptotrema panamense* Hale], *C. discoides* (Stirt.) Lücking, *comb. nov.* [*Graphis discoides* Stirt.], *C. esslingeri* (Hale) Sipman, *comb. nov.* [bas.: *Ocellularia esslingeri* Hale], *C. hiata* (Hale) Sipman, *comb. nov.* [bas.: *Thelotrema hiatum* Hale], *C. pseudoschizostoma* (Hale) Sipman, *comb. nov.* [bas.: *Ocellularia pseudoschizostoma* Hale], *C. referta* (Hale) Lücking, *comb. nov.* [bas.: *Ocellularia referta* Hale], *C. stellata* (Hale) Sipman, *comb. nov.* [bas.: *Leptotrema stellatum* Hale], *Fibrillithecis pachystoma* (Nyl.) Sipman, *comb. nov.* [bas.: *Thelotrema pachystomum* Nyl.], *Leucodecton bisporum* (Nyl.) Sipman & Lücking, *comb. nov.* [bas.: *Thelotrema bisporum* Nyl.], *L. dactyliferum* (Hale) Lücking, *comb. nov.* [bas.: *Ocellularia dactylifera* Hale], *L. sordidescens* (Fée) Lücking & Sipman, *comb. nov.* [bas.: *Trypethelium sordidescens* Fée], *Ocellularia carassensis* (Vain.) Sipman, *comb. nov* [bas.: *Thelotrema carassense* Vain.]., *O. maxima* (Hale) Lumbsch & Mangold, *comb. nov.* [bas.: *Thelotrema maximum* Hale], *R. vulcani* (Hale) Lücking, *comb. nov.* [bas.: *Phaeotrema vulcani* Hale], *Stegobolus anamorphoides* (Nyl.) Lücking, *comb. nov.* [bas.: *Thelotrema anamorphoides* Nyl.], *Stegobolus lankaensis* (Hale) Lücking, *comb. nov.* [bas.: *Ocellularia lankaensis* Hale], *Thelotrema jugale* (Müll. Arg.) Lücking, *comb. nov.* [bas.: *Ocellularia jugalis* Müll. Arg.], and *Wirthiotrema desquamans* (Müll. Arg.) Lücking, *comb. nov.* [bas.: *Anthracothecium desquamans* Müll. Arg.]. All species are described and discussed in detail and illustrated by photographic plates, and keys are provided to genera and species.

Key words: *Amazonotrema*, *Ampliotrema*, Australia, *Chroodiscus*, *Cruentotrema*, *Diploschistes*, *Leptotrema*, *Melanotopelia*, *Melanotrema*, *Myriotrema*, *Nadvornikia*, *Pycnotrema*, *Reimnitzia*, *Rhabdodiscus*, *Schizotrema*, *Stegobolus*, *Topeliopsis*.

Introduction

The lichen family Graphidaceae, as currently circumscribed, was traditionally divided into five separate families: Graphidaceae and Thelotremataceae, as well as Asterothyriaceae, Gomphillaceae, and Solorinellaceae (Wirth & Hale 1963, 1978; Hale 1974, 1978, 1981; Lücking 1997, 2008; Archer 1999, 2000, 2001a-e, 2002, 2003a, b, 2005, 2006; Staiger 2002; Henssen & Lücking 2002; Frisch *et al.* 2006a). Molecular data, however, suggested that these families had to be merged (Staiger *et al.* 2006; Mangold *et al.* 2008a; Rivas Plata & Lumbsch 2011); in a strict monophyletic view, they are now recognized in a single family Graphidaceae, with three subfamilies (Rivas Plata *et al.* 2012a): Fissurinoideae (including parts of the former Graphidaceae and Thelotremataceae), Gomphilloideae (including the former Asterothyriaceae, Gomphillaceae, and Solorinellaceae), and Graphidoideae (including the bulk of the former Graphidaceae and Thelotremataceae). Subfamily Graphidoideae is divided into three tribes: Graphideae (corresponding to the bulk of the former Graphidaceae), Thelotremateae (corresponding largely to the genus *Thelotrema* sensu Hale 1980), and Ocellularieae (corresponding largely to the genera *Myriotrema* and *Ocellularia* sensu Hale 1980). The thus emended Graphidaceae has become the largest family of lichenized fungi together with Parmeliaceae, with probably over 2,000 species worldwide.

The inclusion of Gomphillaceae within Graphidaceae is perhaps not as counterintuitive as it appears at first glance. Typical Gomphillaceae are separated from typical Graphidaceae by the chlorococcoid versus trentepohlioid photobiont, the anastomosing versus unbranched paraphyses, the thin-walled and non-amyloid

versus graphidoid and amyloid ascospores, and the hyphophorous conidiomata, as well as the foliicolous growth habit. However, these differences disappear completely when considering the entire range of variation in both groups: Graphidaceae include taxa with chlorococcoid photobiont (*Diploschistes*) and species with thin-walled, non-amyloid ascospores (*Chroodiscus*, *Acanthotrema*). Other groups, such as *Diorygma*, *Dyplolabia*, and *Ocellularia* s.lat., have at least partially anastomosing paraphyses. Hyphophores are not present in all species of Gomphillaceae and they are completely absent in *Asterothyrium*, *Gyalidea*, and *Psorotheciopsis* (Lücking 2008). Many Gomphillaceae, particularly in the genera *Echinoplaca* and *Gyalideopsis*, are corticolous, and in Graphidaceae, genera such as *Chroodiscus* are exclusively foliicolous. In addition, both groups share important features, such as the usually zeorine, hemiangiocarpous ascomata with a strong tendency to become lobate-lirellate, and the graphidoid ascus type. Therefore, considering the whole range of variation, there is no clear limit between these groups. Notably, *Aulaxina* was maintained in Graphidaceae by Santesson (1952) and *Asterothyrium* at some point was suggested to belong in Thelotremataceae and related to *Chroodiscus* (Vezda & Poelt 1987; Aptroot *et al.* 1994). This view is also supported by the undisputed inclusion of *Diploschistes* in Graphidaceae. This genus is ecologically very different from the remaining Graphidaceae and also genetically distinct, and it had been included in a separate family, Diploschistaceae, in the past. Yet, it is now unanimously accepted as part of Graphidaceae.

Hodkinson (2012) proposed to raise Fissurinoideae to family rank (Fissurinaceae) and maintain, at the same time, the families Thelotremataceae, Gomphillaceae, and Solorinellaceae. While we agree that treating Fissurinaceae at the family rank is an option to retain Gomphillaceae as a separate family, the reinstatement of Thelotremataceae and Solorinellaceae cannot be accepted, as it would be purely schematic. The Thelotremataceae were traditionally separated from the Graphidaceae on account of ascomata morphology (round versus lirellate), this being the only applicable character for their distinction. However, the phylogeny of this group does not allow for such a separation, since several clades (e.g. subfamily Fissurinoideae and tribe Thelotremateae) include both round and lirellate taxa. In addition, the bulk of the taxa formerly included in Thelotremataceae does not form a monophyletic group but is dispersed over several distinct clades (Rivas Plata *et al.* 2012a, c).

In addition to the revised family classification, the generic concepts within the family have also changed dramatically, starting with the monographic treatments by Staiger (2002) and Frisch *et al.* (2006a). Traditionally, ascoma type (rounded, lirellate, pseudostromatic) and ascospore septation (transverse, muriform) and pigmentation (colorless, brown) were used to separate the bulk of the former Graphidaceae and Thelotremataceae into twelve genera: *Ocellularia*, *Thelotrema*, *Phaeotrema*, and *Leptotrema* (all with rounded ascomata), *Graphis*, *Graphina*, *Phaeographis*, and *Phaeographina* (all lirellate), and *Glyphis*, *Medusulina*, *Sarcographa*, and *Sarcographina* (all pseudostromatic). These concepts were originally based on Müller (1880a, b, 1882, 1887a) and further elaborated by Zahlbruckner (1905, 1923), subsequently being used in monographic treatments by Wirth & Hale (1963, 1978), Nakanishi (1966), and Hale (1974, 1978), among others. Based on the work by Salisbury (1971, 1972a, b, 1978), Hale (1980, 1981) presented novel concepts for the taxa with rounded ascomata (former Thelotremataceae), using excipular structure to divide the bulk of the species (excluding *Diploschistes*) into three large genera: *Ocellularia* (excipulum carbonized, lacking periphysoids), *Myriotrema* (excipulum uncarbonized, lacking periphysoids), and *Thelotrema* (excipulum uncarbonized, with periphysoids). All three genera included species with either transversely septate or muriform and colorless or brown ascospores, thus abandoning the previously used ascospore genera.

In the thelotremoid Graphidaceae, Hale's concepts were used until recently when Frisch *et al.* (2006a) applied a combination of thallus, ascoma, ascospore, and chemical features to distinguish 21 genera, and this system was subsequently emended by various authors (Mangold *et al.* 2009; Rivas Plata *et al.* 2010a, b). Molecular studies have much improved our understanding of phylogenetic relationships and generic delimitation within the thelotremoid Graphidaceae, although the delimitation of several genera remains difficult (Frisch *et al.* 2006b; Staiger *et al.* 2006; Mangold *et al.* 2008a; Papong *et al.* 2009a, b; Rivas Plata & Lumbsch 2011; Rivas Plata *et al.* 2012a, b). Five main clades include thelotremoid species formerly classified in Thelotremataceae (Rivas Plata *et al.* 2012a): the *Fissurina* clade (subfamily Fissurinoideae), with the

thelotremoid genera *Clandestinotrema*, *Cruentotrema*, and *Pycnotrema*; the *Topeliopsis* clade (subfamily Graphidoideae tribe Thelotremateae), with the thelotremoid genera *Melanotopelia*, *Nadvornikia*, *Schizotrema*, *Topeliopsis*, and *Wirthiotrema*; the *Diploschistes* clade (subfamily Graphidoideae tribe Thelotremateae), with the thelotremoid genera *Acanthotrema* and *Diploschistes*; the *Thelotrema* clade (subfamily Graphidoideae tribe Thelotremateae), with the thelotremoid genera *Chapsa*, *Chroodiscus*, *Leucodecton*, and *Thelotrema*; and the *Ocellularia* clade (subfamily Graphidoideae tribe Ocellularieae), with the genera *Ampliotrema*, *Fibrillithecis*, *Gyrostomum*, *Leptotrema*, *Melanotrema*, *Myriotrema*, *Ocellularia*, *Redingeria*, *Reimnitzia*, *Rhabdodiscus*, and *Stegobolus*. Thus, in contrast to the four ascospore genera (plus *Chroodiscus* and *Diploschistes*) or the three excipular genera (plus *Diploschistes*) distinguished by previous workers, the thelotremoid taxa within the emended Graphidaceae currently are classified in at least 25 genera. Further genera will certainly be added once the complex situation in the *Ocellularia* clade is resolved (Rivas Plata *et al.* 2012c), and for this clade we have retained the concept laid out by Frisch *et al.* (2006a).

The thelotremoid Graphidaceae are of general interest to ecologists and conservationists as they have been shown to be useful as indicators of ecological continuity (forest health) in tropical forest ecosystems (Hale 1974, 1978, 1981; Rivas Plata *et al.* 2008a). In particular the taxa with glossy, corticate, greenish thalli (*Myriotrema-Ocellularia* type) appear to be restricted to more or less undisturbed forest vegetation and preferrably grow on the trunks of large trees. Rivas Plata *et al.* (2008a) suggested a protocol to use morphotypes instead of taxa to assess the condition of a forest plot or fragment; in this protocol, all species with *Myriotrema-Ocellularia* type thalli are included and distinguished based on ascoma morphology, including shape, carbonization, and columella structures.

Costa Rica is an ideal area to study these lichens as it has an extensive system of protected areas covering different types of vegetation (Holdridge 1967, 1982; Holdridge *et al.* 1971; Gómez 1986; Hartshorn 1991). In spite of its comparatively small area, it harbours an extraordinary richness of lichenized fungi, with somewhere between 2,400 and 2,800 species (Lücking *et al.* 2004, 2009a). Our first treatment of Graphidaceae revealed 115 species in the genus *Graphis* alone (Lücking *et al.* 2008a), which represents about one third of all species currently known world-wide (Lücking *et al.* 2009b). The thelotremoid Graphidaceae are no exception: of the roughly 600 species currently accepted world-wide, 186 have been found in Costa Rica and another 30 in adjacent areas, thus expected to occur in Costa Rica. This is more species than known from Australia (173; Mangold *et al.* 2009), which is 250 times the size of Costa Rica. The bulk of the material included here was gathered in the framework of our TICOLICHEN biodiversity inventory (Lücking *et al.* 2004, 2008a; http://www.nsf.gov/awardsearch/showAward.do?AwardNumber=0206125), with over one thousand specimens pertaining to the thelotremoid Graphidaceae. Additional collections housed in B and F (previous trips by H.J.M. Sipman, R. Lücking, and participants of the 1978/79 IAL excursion to Costa Rica), FH (collections made C.W. Dodge and A. M. Brenes and collaborators), G (collections made by H. Pittier and A. Tonduz, mostly studied by Müller Argoviensis), MEL (collections made by R. Filson), US (collections by M. E. Hale), and the local herbaria in Costa Rica (CR, INB, USJ), were also studied.

Study Area

Costa Rica is located on the southern part of the Central American land bridge (Fig. 1), covering an area of 51,100 km^2. The territory also includes Cocos Island, the only wet oceanic island in the eastern Pacific, situated about 500 km southwest of the mainland. The country is divided into a Pacific and Atlantic watershed by a series of mountain ranges, the Cordilleras of Guanacaste, Tilarán, Volcánica Central, and Talamanca. The highest elevation is Cerro Chirripó with 3,819 m in the Cordillera de Talamanca. The Cordilleras in Guanacaste and Tilarán and the Cordillera Volcánica Central are composed of ancient and partly active volcanoes (Pichler & Weyl 1975; Abratis & Wörner 2001; Marshall *et al.* 2003).

The climate in the country is oceanic (Herrera 1985; Coen 1991), receiving between 3,000 and 6,000 mm annual precipitation in the wet lowlands, with a marked dry season on the Pacific side between January and

March. The northwestern Pacific lowlands are comparatively dry, with 1,300 to 2,000 mm annual precipitation and a marked dry season from December to April. The montane ranges of the Atlantic slopes receive extremely high annual precipitation up to 7,000 mm.

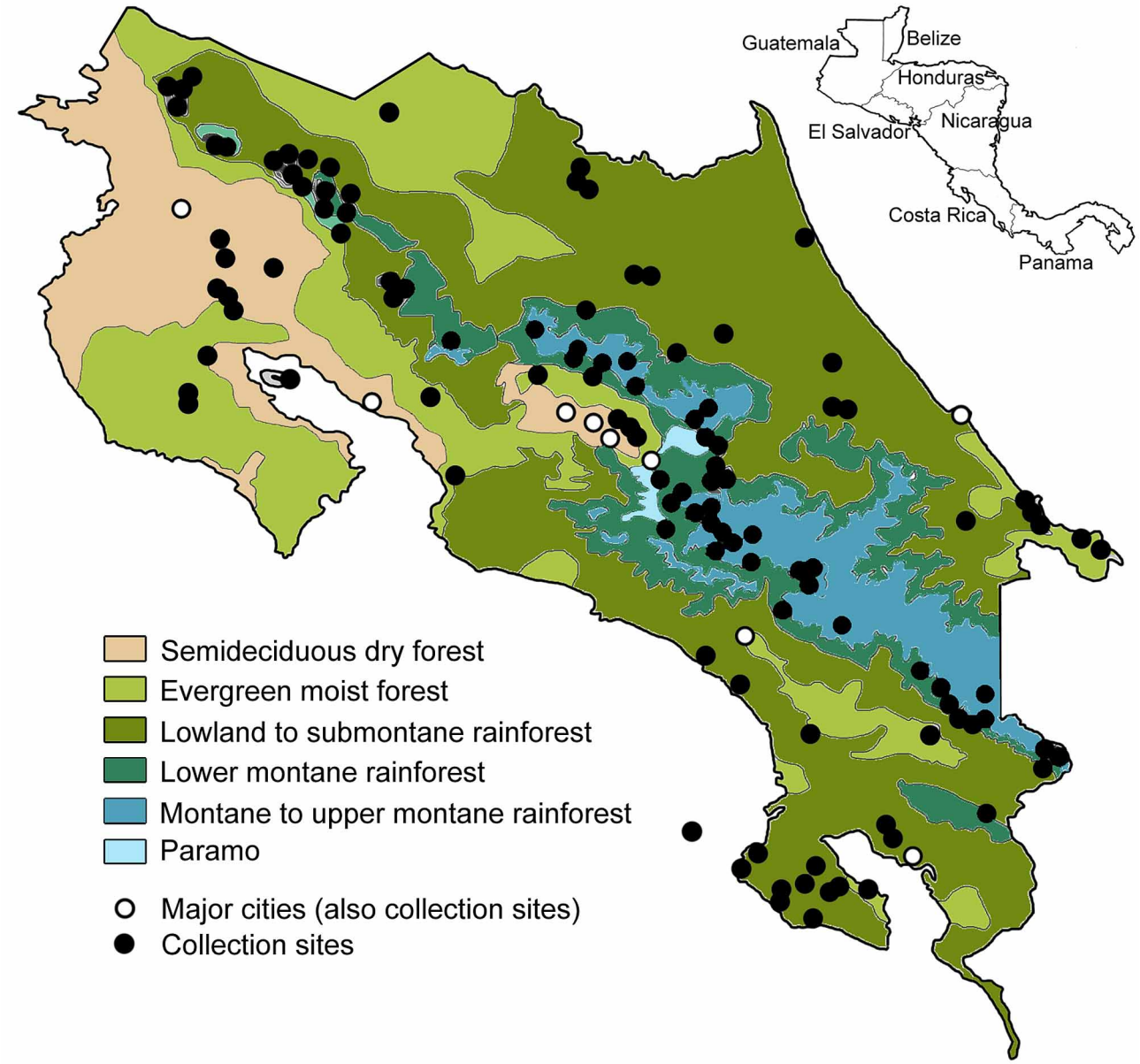

FIGURE 1. Map of Costa Rica showing collection sites in relation to major vegetation types.

According to Holdridge *et al.* (1971) and Hartshorn (1991), Costa Rica shares 12 of the 38 world life zones defined by Holdridge (1967, 1982), comprising tropical rain, wet, moist, and dry forest, with the corresponding altitudinal subdivisions (lowland, premontane, lower montane, montane), as well as subalpine rain paramo. The 12 life zones can be merged into six main ecozones which differ in their lichen diversity and species composition, also with respect to Graphidaceae (Fig. 1, 2): semideciduous dry forest, evergreen moist forest, lowland to submontane rain forest, lower montane rain forest, montane to upper montane rain- and cloudforest, and paramo. Gómez (1986) distinguished 53 macrovegetation types based on physiognomy and species composition. These also include savannas reminescent of the Brazilian Cerrado, which support a high diversity of Graphidaceae.

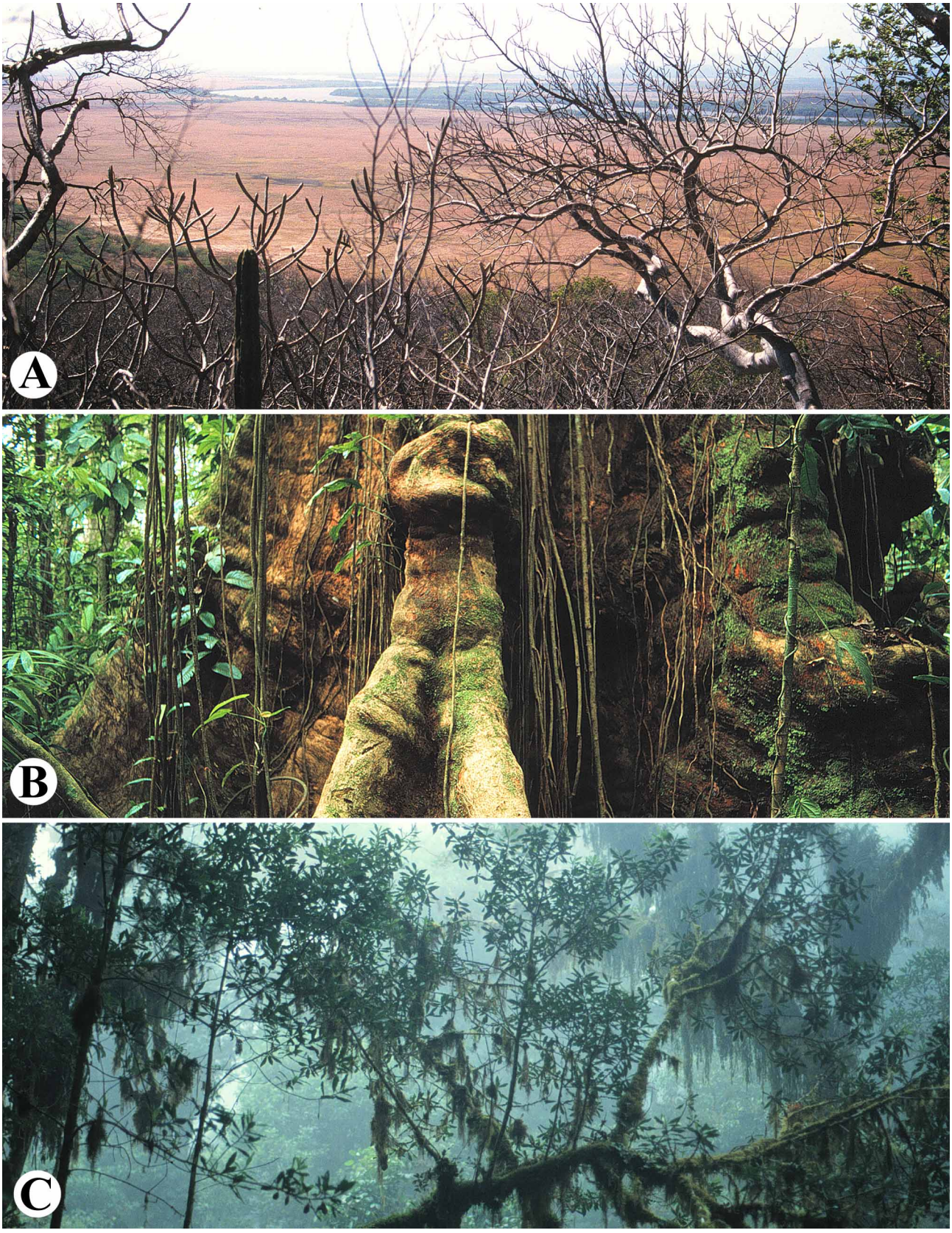

FIGURE 2. Selected major vegetation types with occurrence of thelotremoid Graphidaceae. A. Tropical dry forest in Guanacaste (common are species of *Leucodecton*). B. Lowland rain forest at La Selva Biological Station (common are species of *Myriotrema*, *Ocellularia*, and *Stegobolus*). C. Upper montane cloud forest in the Cordillera de Talamanca (common are species of *Clandestinotrema* and *Thelotrema*).

Costa Rica is considered one of the 20 countries representing biodiversity hotspots in the world (Janzen 1974; Groombridge 1994; Gámez *et al.* 1997; Obando 2002). Its total number of species is estimated at 500,000, of which 360,000 are supposed to be insects (Obando 2002). Fungi represent the second largest group, with 65,000 expected species. Because of its small size, just 0.5% of that of the United States, Costa Rica exhibits the highest species density among megadiverse countries such as Mexico, Colombia, Brazil, Indonesia, and Australia (García 1997; Obando 2002). The first systematic flora of Costa Rica, *Primitiae Florae Costaricensis*, was initiated by the Swiss engineer Henry François Pittier, and this work included a substantial treatment of lichens (Müller 1891, 1893). National and international organizations subsequently shaped the development of scientific expertise in Costa Rica, including the National Museum, the Tropical Agricultural Center for Research and Teaching (CATIE), the Tropical Science Center, the National Park Service, and especially the Organization for Tropical Studies (OTS). Eventually the Missouri Botanical Garden (MOBOT) became a driving force behind the systematic inventory of Costa Rican plants and in the foundation of the National Biodiversity Institute (INBio) in 1989, which since then is cataloging Costa Rica's biodiversity. Fungi are the least known group besides bacteria and viruses; of the 65,000 species expected to occur in the country, only about 3,500 are known to date (Obando 2002; Lücking *et al.* 2004, 2009a; Halling & Mueller 2005). This number is expected to raise substantially due to the effort of INBio and its collaborating institutions, to systematically explore the fungal and lichen biota of Costa Rica (Kappelle & Sipman 1992; Lücking 1992, 1995, 1999; Mueller & Halling 1995; Gómez 1996; Halling 1996; Carranza & Mueller 1996; Mata 1999; Umaña & Sipman 2002; Huhndorf *et al.* 2003; Mata *et al.* 2003; Chaves *et al.* 2004; Fernández *et al.* 2004; Grube *et al.* 2004; Rogers *et al.* 2004; Halling & Mueller 2005; Aptroot *et al.* 2006, 2008; Lücking *et al.* 2006, 2007a, b; Nelsen *et al.* 2006, 2007; Rivas Plata *et al.* 2006). Preliminary results with regard to lichenized fungi indicate a diversity that by far exceeds expectations (Lücking *et al.* 2006, 2008a, 2009a).

Costa Rica has a long-standing tradition of protecting its natural resources. Since 1994, the protected areas are arranged in conservation areas administered under the National System of Conservation Areas (SINAC). SINAC oversees more than 160 protected areas which cover about 25% of the country's surface. Until the late 1980's, Costa Rica was one of the countries in the world with the highest deforestation rate, with only about 25% of forest left (Fournier 1985; Porras & Villareal 1985; García 1997). Conservation efforts increased during the 1980's and the deforestation rate decreased from 60,000 ha per year in 1980 to presently less than 5,000 ha per year (García 1997; Obando 2002). As a result, forest cover increased to almost 45%, although many of the recovered areas were planted with fast-growing exotic trees, such as *Eucalyptus*. Lichens can be used as bioindicators of ecological continuity of tropical forests, to assess the state of forest fragments and regrowth (Wolseley & Aguirre-Hudson 1991; Wolseley *et al.* 1994; Rivas Plata *et al.* 2008a), and the mosaic of undisturbed and disturbed forest and forest regrowth found within many of the protected areas in Costa Rica makes this country a primary target for such studies and implementations.

Previous Reports of Thelotremoid Graphidaceae from Costa Rica

Few authors have reported thelotremoid Graphidaceae (Thelotremataceae) from Costa Rica, the most important being Müller (1891, 1893), Breuss (2000, 2001, 2004, 2006, 2008), and Breuss & Neuwirth (2007). Dodge (1933) started a treatment of lichens collected by himself and colleagues but never proceeded to publish the crustose taxa; nevertheless, numerous identified collections are housed at FH and these are included here to clarify their status. Including these, 49 names of thelotremoid Graphidaceae have been reported from or cataloged for Costa Rica, including seven newly described species (Table 1). However, only 14 were correctly identified using the currently accepted species concepts.

TABLE 1. Species of thelotremoid Graphidaceae previously reported from Costa Rica or housed at FH. Newly described taxa based on Costa Rican type material are marked with an asterisk(*).

Originally reported name	Reference	Correct name or identification
Chroodiscus coccineus (Leight.) Müll Arg.	unpublished record (FH)	confirmed
Leptotrema bahianum (Ach.) Müll. Arg.	Müller 1893	*Ocellularia bahiana*
Leptotrema compunctum (Ach.) Müll. Arg.	Müller 1891	*Leucodecton occultum*
Leptotrema compunctum var. *purpuratum* Müll. Arg.*	Müller 1891	*Leucodecton occultum*
Leptotrema develatum (Nyl.) Zahlbr.	unpublished record (FH)	*Leucodecton occultum*
Leptotrema develatum (Nyl.) Zahlbr.	unpublished record (FH)	*Ocellularia bahiana*
Leptotrema glaucescens v. *epileptum* (Nyl.) Zahlbr.	unpublished record (FH)	*Reimnitzia santensis*
Leptotrema leucocarpoides (Nyl.) Zahlbr.	unpublished record (FH)	*Leucodecton reclusum*
Leptotrema metaphoricum (Nyl.) Zahlbr.	unpublished record (FH)	*Stegobolus metaphoricus*
Leptotrema microsporum Zahlbr.	unpublished record (FH)	*Stegobolus metaphoricus*
Leptotrema polyporum Riddle	unpublished record (FH)	*Leucodecton glaucescens*
Leptotrema postpositum (Nyl.) Zahlbr.	unpublished record (FH)	*Thelotrema lepadinum*
Leptotrema wightii (Tayl.) Müll. Arg.	Müller 1893	*Leptotrema wightii*
Leptotrema wightii (Tayl.) Müll. Arg.	unpublished record (FH)	*Ocellularia obturascens*
Leptotrema wightii (Tayl.) Müll. Arg.	unpublished record (FH)	*Stegobolus subemersus*
Myriotrema album Fée	Breuss 2000	*Myriotrema album*
Myriotrema compunctum (Ach.) Hale	Kalb 1988	*Leucodecton occultum*
Ocellularia alborosella (Nyl.) R. Sant.	Breuss 2000	*Chapsa alborosella*
Ocellularia auberianoides (Nyl.) Müll. Arg.	unpublished record (FH)	*Stegobolus auberianus*
Ocellularia auratipruinosa Breuss*	Breuss 2000	*Ampliotrema dactylizum*
Ocellularia bonplandii Spreng.	Müller 1891	*Ocellularia* cf. *perforata*
Ocellularia bonplandii Spreng.	unpublished record (FH)	*Porina nucula*
Ocellularia cinchonarum var. *verrucosa* (Fee) Müll. Arg.	unpublished record (FH)	*Ocellularia cavata*
Ocellularia cinchonarum var. *verrucosa* (Fee) Müll. Arg.	unpublished record (FH)	*Porina* sp
Ocellularia costaricensis Müll. Arg.*	Müller 1891	*Myriotrema costaricense*
Ocellularia costaricensis Müll. Arg.	unpublished record (FH)	*Stegobolus wrightii*
Ocellularia crispata Müll. Arg.	unpublished record (FH)	*Chapsa sublilacina*
Ocellularia excavata var. *impressula* (Vain.) Zahlbr.	unpublished record (FH)	*Thelotrema leucomelaenum*
Ocellularia inaequata (Nyl.) Zahlbr.	unpublished record (FH)	*Ochrolechia* spec.
Ocellularia isertii (Vain.) Zahlbr.	unpublished record (FH)	*Porina americana*
Ocellularia lepadinoides (Leight) Zahlbr.	unpublished record (FH)	*Myriotrema* spec.
Ocellularia lepadinoides (Leight) Zahlbr.	unpublished record (FH)	*Thelotrema* spec.
Ocellularia leucomelaena (Nyl.) Hale	Kalb 1988	*Clandestinotrema leucomelaenum*
Ocellularia myriopora [as '*myriospora*'] Müll. Arg.	Müller 1891	*Myriotrema album*
Ocellularia papillata (Leight.) Zahlbr.	Breuss 2001	confirmed
Ocellularia perforata (Leight.) Müll. Arg.	Breuss 2000	confirmed
Ocellularia phlyctellacea Müll. Arg.*	Müller 1893	*Chapsa chionostoma*
Ocellularia phlyctellacea Müll. Arg.	unpublished record (FH)	*Porina mastoidea*
Ocellularia phlyctellacea Müll. Arg.	unpublished record (FH)	*Porina* spec.
Ocellularia plurifaria (Nyl.) Müll. Arg.	Müller 1891	*Myriotrema plurifarium*
Ocellularia rhodostroma (Mont.) Zahlbr.	Breuss 2000	confirmed
Ocellularia rufocincta Müll. Arg.*	Müller 1893	*Ocellularia perforata*
Ocellularia rufocincta Müll. Arg.	unpublished record (FH)	*Ocellularia* spec.
Ocellularia schizostoma (Tuck.) Müll. Arg.	unpublished record (FH)	*Trypethelium nitidiusculum*
Ocellularia terebratula (Nyl.) Müll. Arg.	unpublished record (FH)	*Myriotrema clandestinum*
Ocellularia umbilicata Müll. Arg.*	Müller 1893	confirmed
Phaeotrema auberianum (Mont.) Müll. Arg.	unpublished record (FH)	*Stegobolus metaphoricus*
Phaeotrema consimile Müll. Arg.	Müller 1893	*Thelotrema* cf. *lacteum*
Phaeotrema domingense (Fee) Müll. Arg.	unpublished record (FH)	*Ocellularia rhodostroma*
Phaeotrema fuscescens (Kremp.) Zahlbr	unpublished record (FH)	*Chapsa neei*
Phaeotrema jamaicense Müll. Arg.	unpublished record (FH)	*Thelotrema hiatum*
Phaeotrema leucocarpum (Nyl.) Müll. Arg.	unpublished record (FH)	*Thelotrema* spec.
Phaeotrema meiospermum (Nyl.) Müll. Arg.	unpublished record (FH)	*Reimnitzia santensis*
Thelotrema depressum Mont.	unpublished record (FH)	*Ocellularia subpraestans*
Thelotrema leucomelaenum Nyl.	unpublished record (FH)	*Thelotrema subtile*
Thelotrema myrioporoides Müll. Arg.*	Müller 1893	*Myriotrema myrioporoides*
Thelotrema myrioporoides Müll. Arg.	unpublished record (FH)	*Myriotrema subconforme*
Thelotrema velatum Müll. Arg.*	Müller 1893	*Chapsa discoides*

Material and Methods

The collections treated here were chiefly made during three TICOLICHEN field campaigns in summer 2002, spring 2003 and spring 2004, but also during previous trips by H. J. M. Sipman, R. Lücking, and K. Kalb, as well as other participants of the 1978/79 IAL excursion to Costa Rica. Identification work was done at the National Institute for Biodiversity (INBio) in Costa Rica, the Field Museum of Natural History in Chicago, U.S.A, the Botanical Garden & Botanical Museum Berlin-Dahlem in Germany, and the Adviesbureau voor Bryologie en Lichenologie in the Netherlands. At the Field Museum of Natural History, specimens were examined using LEICA MS5 and OLYMPUS SZX12 dissecting microscopes and ZEISS Axioscop 2 and OLYMPUS BH-2 compound microscopes, in part connected to JENOPTIC ProgRes C3 and C5 digital microscope cameras. Images were also made with a NIKON F301 SLR film camera and NIKON Coolpix 5400 and NIKON Coolpix 8400 digital cameras. The investigated specimens are mostly kept in the herbaria B, BR (formerly in ABL), CR, F, FH, INB, U, US, and USJ, as indicated.

Anatomical measurements refer to specimens mounted in water. For iodine reactions, we used FLUKA 62650 Lugol solution. Spot tests with P (for psoromic and protocetraric acids) were done on small, separated pieces of thalli with the cortex scraped off, using *para*-phenyldiamine crystals freshly dissolved in alcohol. Spot tests with C (for lecanoric acid) were performed with household bleach also on thallus pieces with the cortex scraped off. Spot tests with K (for norstictic and stictic acids) were done under the compound microscope using sections of thalli and ascomata. For specimens hold at B, BR (initially ABL), F, FH, and US, we also employed thin-layer chromatography (TLC) using solvent C (White & James 1985; Orange *et al.* 2001; Lumbsch 2002). Types were restudied chemically only if no previous TLC annotation labels were available or reports on the chemistry were doubtful.

For ascospore measurements, we measured 20 mature ascospores per thallus randomly selected from sections of three separate apothecia. Differences in ascospore size used here to distinguish species (if the main distinguishing character) are in the range of at least 50–100% of the taxon with the smaller ascospores, e.g. 20–30 µm versus 30–50 µm as a typical case. Because of this, we did not perform statistical tests, which are meaningful to detect minor range differences but are not practical for taxonomic purposes: with sufficient sampling (100 or more ascospores), even differences of only 1 µm (e.g. 15–20 µm versus 16–21 µm) result in statistical significance but cannot be employed in a key or a discriminating species description.

Nomenclature follows Frisch (2006), Frisch & Kalb (2006), and Rivas Plata *et al.* (2010a, b) as far as species are treated by these authors. Many new combinations are proposed, but for certain taxa, further data must be awaited for proper generic placement. This concerns in particular the genera *Myriotrema* s.lat., *Ocellularia* s.lat., and *Stegobolus* s.lat. (Rivas Plata *et al.* 2012b). Type material was studied for all species and their accepted synonyms, except when noted otherwise; types seen are marked with "!". For newly described species, it is implied that the types were studied by us and therefore these are not specifically marked.

Diversity of Thelotremoid Graphidaceae in Costa Rica

A total of 186 species of thelotremoid Graphidaceae in 23 genera are here reported for Costa Rica, plus an additional 30 taxa for adjacent areas (El Salvador, Nicaragua, Panama) and expected to occur in Costa Rica. This is the highest number of thelotremoid Graphidaceae reported for any country in the world thus far, followed by Australia (173 species; Mangold *et al.* 2009), Sri Lanka (130 species; Hale 1981; Weerakoon *et al.*, in prep.), and Panama (110 species; Hale 1978; Lumbsch *et al.* 2011; Lücking *et al.*, in prep.). The much higher number of species found in Costa Rica compared to Panama could be in part due to different collection efforts: in the frame of the Ticolichen project, three larger expeditions with a team of experienced personnel were made, plus further field trips by HJMS and RL, extensive field work by JLC, as well as field work by Breuss (2000, 2001, 2004, 2006, 2008) and others. In contrast, the information for Panama is almost

exclusively based on three field trips by Hale (1978). On the other hand, Hale concentrated on the thelotremoid taxa and paid much attention to logging sites in primary forest, the most effective way to find these lichens. In Costa Rica no such sites have been investigated as they are rare and difficult to access; therefore, our results probably still underestimate the true diversity of this group of lichens.

Together with our previous treatment of the genus *Graphis* (Lücking *et al.* 2008a), a total of 293 species of Graphidaceae (excluding Gomphilloideae) have now been reported for Costa Rica. The remaining graphidoid groups, including genera such as *Diorygma*, *Fissurina*, *Glyphis*, and *Phaeographis* and allies, will probably add over one hundred additional species, raising the total number of Graphidaceae for the country to over 400. For Australia, a country 150 times as large as Costa Rica, a total of 336 Graphidaceae (including Thelotremataceae but excluding Gomphilloideae) have been reported (Archer 2009; Mangold *et al.* 2009).

Taxonomic Treatment

In the following account, the genera and species are listed in alphabetical order. Keys are presented to all genera and species. Of the 26 genera of thelotremoid Graphidaceae currently accepted (including one described herein), 23 were found in Costa Rica. *Amazonotrema* Kalb (Kalb 2009) is possibly endemic to the Amazon rain forest, and *Melanotopelia* has so far only been found in the temperate to subantarctic southern hemisphere (Mangold *et al.* 2008b; Lumbsch *et al.* 2010). However, the absence of *Topeliopsis* is remarkable; this genus is expected to occur at high elevations over bryophytes and dead plants and possibly has been overlooked. The only *Topeliopsis*-like species, both in morphology and ecology, found so far in Costa Rica is actually a *Chapsa*, *C. meridensis*.

The delimitation of genera based on molecular data makes it more difficult to key out each genus clearly using morphological data alone, a problem that is now widely appreciated in fungal and lichen taxonomy but is, unfortunately, a reality that has to be accepted if we aim at delimiting natural rather than artificial taxa. In cases where species might key out under genera that are morphologically similar, we have keyed out such species also under the different genus keys.

Key to the Genera of Thelotremoid Graphidaceae Found in Costa Rica (23)

For general terminology, see Frisch *et al.* (2006). Before using this key, it is strongly recommended to analyse the chemistry of material by means of TLC. Spot tests are usually a good indication of the principal substances present, but they are not always reliable, may not discriminate between different substances, cannot indicate satellite or mixed substances present, and for many secondary compounds, no spot tests are known. For the species treated here, a total of 13 different main substances were detected, and while some of them can be readily identified using spot tests, for others TLC is recommended or required (Table 2).

The thallus cortex is best observed in transverse sections (Fig. 3A–C) but can also be judged to some extent from the appearance of the surface. Inclusion of calcium oxalate crystals can appear as irregular or columnar clusters or as small warts (Fig. 3C–E). The columnar clusters in transverse sections are in fact a network of crystalline walls separating chambers of photobiont cells, and the thallus in such species appears characteristically grainy, e.g. in *Leptotrema wightii* (Fig. 14A). That species also features red medullary crystals (Fig. 3F). A gall-forming thallus is here defined as thallus which bulges over the substrate and is hollow underneath; the hollow part is often colonized by ants. A typical example would be *Leptotrema wightii*. This definition is slightly different from what is often found in Trypetheliaceae, in which the lichen thallus causes the bark periderm to swell and therefore appears bulging over the substrate; the periderm may then be excavated by ants. Since the thalli in both cases appear similar, we apply the term gall-forming to both cases. Mazaediate ascomata in which the ascospores are deposited as dry black mass above the hymenium (Fig. 3G–H) are only known from one species in this treatment, *Nadvornikia hawaiiensis*. The excipulum is

either paraplectenchymatous (Fig. 3I) or prosoplectenchymatous and often brown to carbonized. In order to determine the degree of carbonization, it is best to study a partially sectioned ascoma under the stereomicroscope. The term carbonized is here restricted to structures that appear black (Fig. 3J–L), not (light to dark) brown. Crystal-filled structures that appear white under the stereomicroscope may look dark grey or black under the microscope, although they are obviously not carbonized. Periphysoids are more or less horizontal hyphae emerging from the lateral excipulum towards the hymenium (Fig. 3M); in some species, either periphysoids or paraphyses or both have spinulose tips (Fig. 3N). Inspersed hymenia have irregularly shaped oil droplets densely lining the paraphyses (Fig. 3O–P); when sectioning an ascoma, sectioned ascospores often release oil into the medium which forms dispersed, regularly round droplets not associated with the paraphyses; this is not considered inspersion.

TABLE 2. Main secondary substances in species found or expected to occur in Costa Rica, and their detection using spot tests and/or TLC. The spot test should be applied as indicated in material and methods and in this table; they are not repeated in the keys and descriptions. Numbers in the second column indicate the number of species in which the substance was found as main component (several species have more than one main substance, e.g. hypoprotocetraric acid and lichexanthone or psoromic and stictic acids); 69 species have no secondary substances.

Main substance	Species	K (microscope section)	P (exposed medulla)	C (exposed medulla)	UV (thallus surface)	TLC
Lichexanthone	8	K–	P–	C–	UV+ yellow	optional
Lecanoric acid	3	K–	P–	C+ red	UV–	optional
Stictic acid	41	K+ yellow efflux (bright cadmium yellow)	P+ orange	C–	UV–	optional
Norstictic acid	3	K+ yellow efflux forming red crystals	P+ orange	C–	UV–	optional
Psoromic acid	48	K–	P+ bright yellow	C–	UV–	optional
Protocetraric acid	20	K+ faint dirty yellow efflux (in high concentrations)	P+ orange-red	C–	UV–	optional
Hypoprotocetraric acid	20	K–	P–	C–	UV–	required
Olivaceic acid	1	K+ red efflux	P–	C–	UV–	optional
Cinchonarum unknown	6	K–	P–	C–	UV–	required
Reconditus unknown	1	K–	P–	C–	UV–	required
Viridis unknown	1	K–	P–	C–	UV–	required
Subpsoromic acid	1	K–	P+ yellow-orange	C–	UV–	required

When observing ascospores, one should try to reconstruct ascospore ontogeny and only take into account mature ascospores for measurements, color, and microscopic reactions (amyloidity). Mature ascospores have the endospore, if present, well-developed. Characters to be observed include the number and arrangement of septa, the nature of the septa in mature ascospores, the color of the septa and wall (the lumen usually remains unpigmented), and the I-reaction or amyloidity (Fig. 4A–P).

1. Ascomata present 2
- Ascomata absent; identification by means of vegetative propagules (soralia, isidia, schizidia) 33

2. Ascomata mazaedial, with ascospores accumulating as dry black mass above the hymenium ..... ***Nadvornikia* (*hawaiiensis*)**
- Ascomata apothecial, perithecioid or lirellate 3

3. Ascomata perithecioid (remaining closed for a long time), vividly dark red from the outside ..... ***Enigmotrema***
- Ascomata of variable shapes, if perithecioid then with distinct pore, if bright (dark) red then with exposed disc or exposed medulla of thallus covering the disc 4

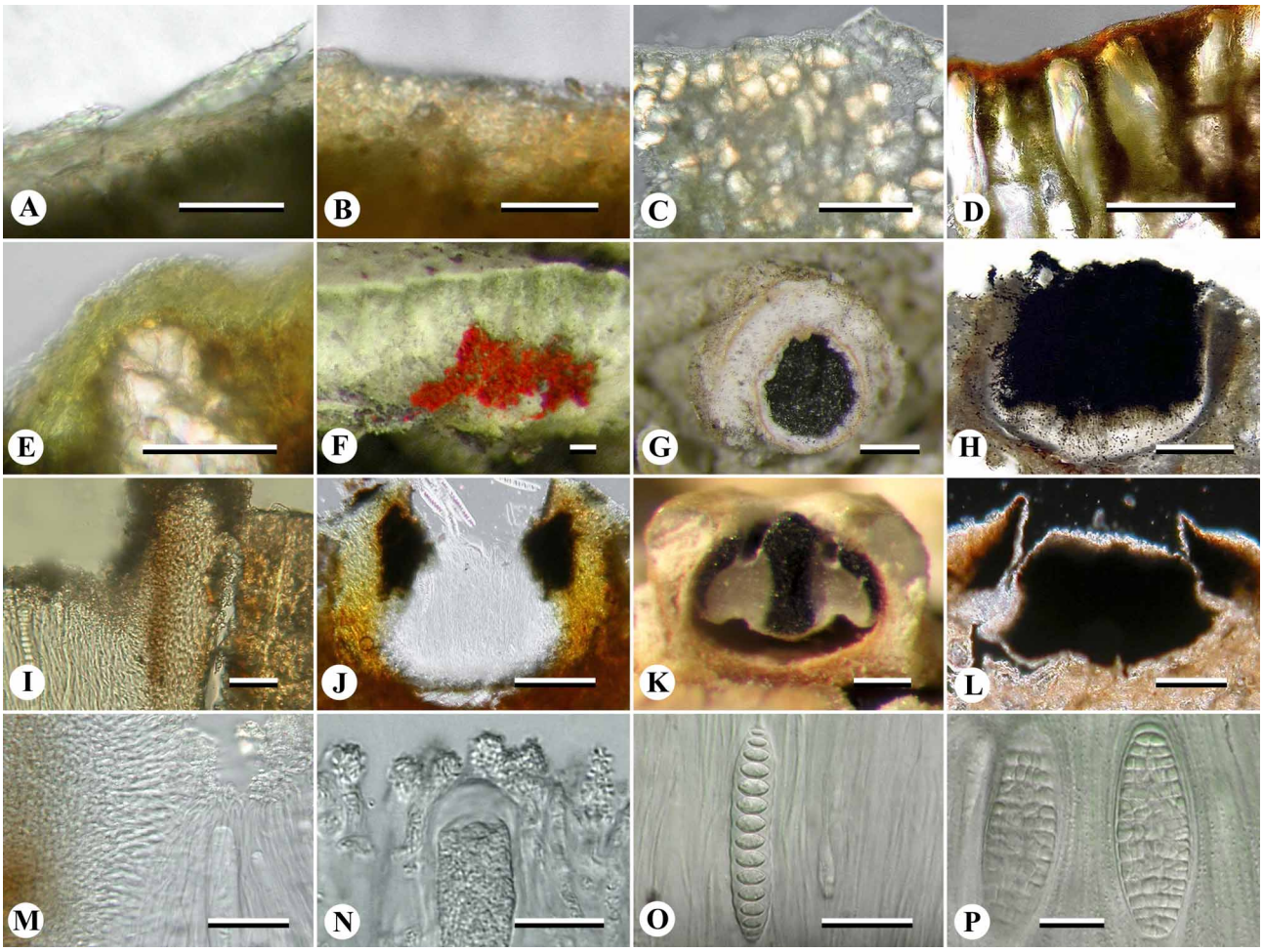

FIGURE 3. Anatomical details in thelotremoid Graphidaceae. A. Cortex prosoplectenchymatous and splitting (e.g. *Myriotrema*). B. Cortex paraplectenchymatous (e.g. *Ampliotrema*). C. Calcium oxalate crystals in irregular clusters. D. Calcium oxalate crystals in vertical columns (e.g. *Leptotrema wightii*). E. Calcium oxalate crystals in verruciform clusters. F. Red medullary crystals (*Leptotrema wightii*). G–H. Mazaedium (*Nadvornikia hawaiiensis*). I. Paraplectenchymatous excipulum (e.g. *Thelotrema*). J. Apically carbonized excipulum. K. Fully carbonized excipulum and finger-like columella. L. Broad-stump-shaped columella (e.g. *Melanotrema*). M. Lateral periphysoids (*Chapsa*, *Thelotrema*). N. Apically spinulose paraphyses (*Acanthotrema*). O. Clear hymenium. P. Inspersed hymenium with oil droplets lining the paraphyses. Scale = 20 µm except G–H = 500 µm and J–L = 200 µm and N = 10 µm.

4. Growing on inorganic substrata (soil, rock) or over bryophytes (then thallus well-developed); lecanoric acid; photobiont chlorococcoid ..... ***Diploschistes***
- Growing on organic substrata; if over bryophytes, then thallus reduced and thin; lecanoric acid absent; photobiont trentepohlioid 5

5. Growing on leaves; apothecia chroodiscoid (with erect to recurved marginal lobules and exposed disc), with colorless excipulum and lacking periphysoids; photobiont of *Phycopeltis* type, with rectangular to elongate cells in more or less radiate rows ..... ***Chroodiscus***
- Growing on bark or rarely on wood or bryophytes; apothecia variable, if chroodiscoid then either with brown to carbonized excipulum or with periphysoids; photobiont of *Trentepohlia* type, with elongate to rounded cells in short threads or irregular groups 6

6. Apothecia chroodiscoid, with brightly pigmented disc and carbonized excipulum; periphysoids absent 7
- Apothecia variable, if chroodiscoid then with unpigmented disc and uncarbonized, colorless to brown excipulum; periphysoids mostly present 9

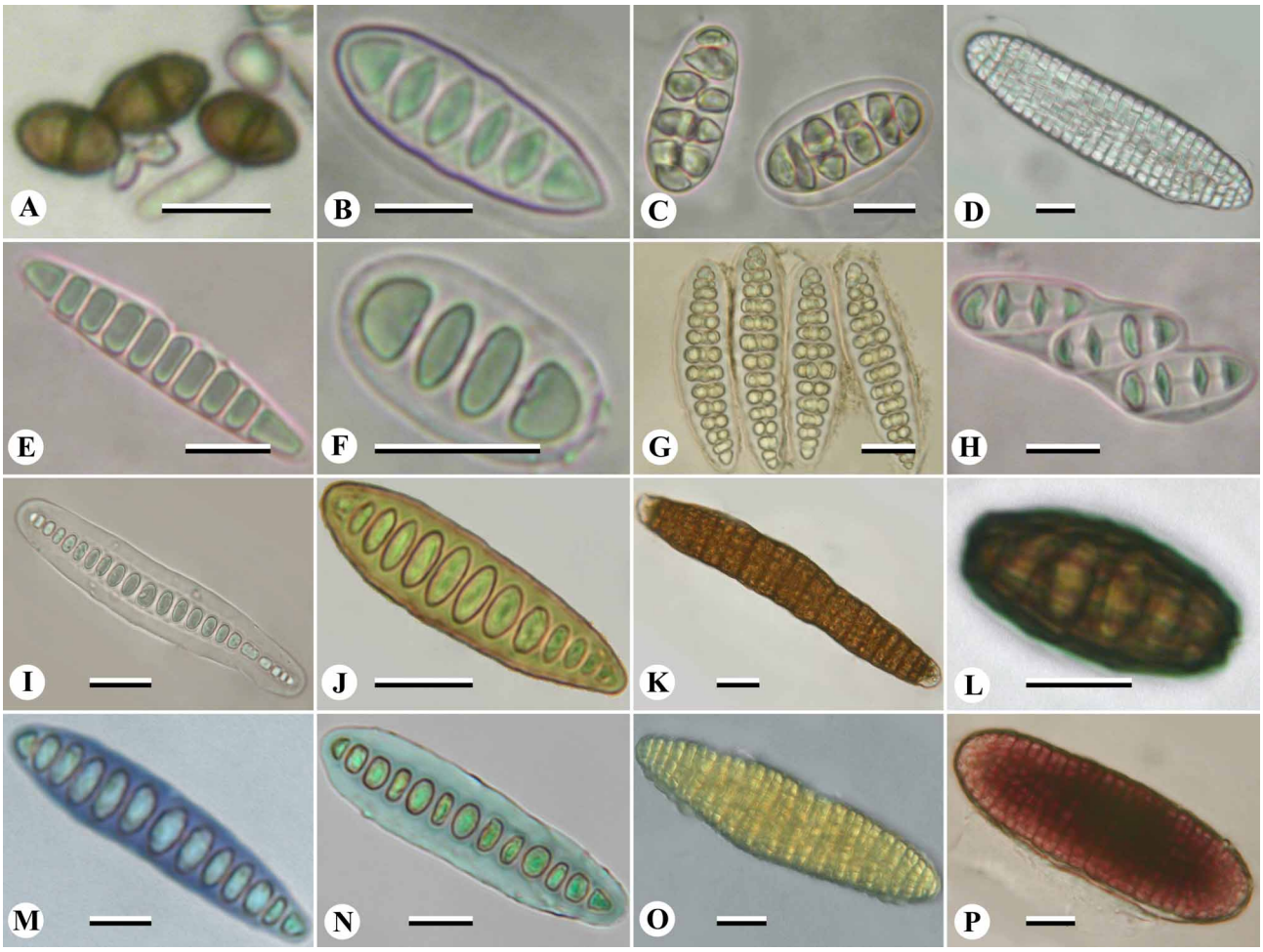

FIGURE 4. Ascospore types in thelotremoid Graphidaceae. A. Ascospores 1-septate (*Nadvornikia hawaiiensis*). B. Ascospores transversely septate. C. Ascospores submuriform (*Cruentotrema cruentatum*). D. Ascospores richly muriform. E. Ascospores subdistoseptate with rather thin septa and almost rectangular lumina. F. Ascospores distoseptate with thick septa and lens-shaped lumina. G. Ascospores distoseptate with rounded lumina and thick outer walls (*Thelotrema lepadinum*). H. Ascospores with thick septa and diamond-shaped lumina (*Clandestinotrema*, *Cruentotrema*). I. Ascospores hyaline. J. Ascospores light brown. K. Ascospores dark brown. L. Ascospores dark brown and ornamented (e.g. *Redingeria*). M. Ascospores amyloid. N. Ascospores weakly amyloid. O. Ascospores non-amyloid (the yellow iodine solution filling the lumina. P. Ascospores hemiamyloid (e.g. *Topeliopsis*). Scale = 10 µm except D, G, I–K and O–P = 20 µm.

7. Hymenium strongly inspersed; protocetraric acid ..... ***Ampliotrema* p.p.**
- Hymenium clear; no substances except apothecial pigments 8

8. Apothecial disc (exposed medulla of thallus covering apothecia) dark red (isohypocrellin); excipulum simple; ascospores submuriform, I–, with angular to diamond-shaped lumina ..... ***Cruentotrema* (*cruentatum*)**
- Apothecial disc yellow-orange or cinnabar-red (unspecified anthraquinones); excipulum in concentric layers alternating with old hymenia, with the newest hymenium forming a narrow rim at the periphery of the disc; ascospores transversely septate, I+ violet-blue, with lens-shaped lumina ..... ***Gyrotrema***

9. Apothecia with columella structures (columns of sterile tissue covering or penetrating the hymenium) 10
- Apothecia lacking columella structures 15

10. Ascospores colorless, I–, with angular to diamond-shaped lumina resembling ascospores of *Astrothelium*; primary septum thickened before the appearance of additional septa ..... ***Clandestinotrema* p.p.**
- Ascospores colorless to brown, I+ violet-blue when colorless or young, with lens-shaped to rounded lumina; primary septum thickened after the appearance of additional septa 11

11. True columella absent (not penetrating the hymenium), but irregular pseudocolumella above the hymenium present 12
- True columella present, penetrating the hymenium from below 13

12. Excipulum and columella colorless ..... ***Myriotrema* p.p.**
- Excipulum brown to carbonized, columella colorless to brown ..... ***Ocellularia* p.p.**

13. Columella simple to broad (but not truncated), more or less finger-like ..... ***Ocellularia* p.p.**
- Columella broad-stump-shaped (truncated) to lobate-reticulate or becoming divided 14

14. Thallus cortex loose, surface often irregular to grainy, yellowish to brownish grey ..... ***Redingeria***
- Thallus cortex dense, often splitting, surface more or less smooth, greenish to olive-brown ..... ***Stegobolus***

15. Periphysoids present 16
- Periphysoids absent 19

16. Paraphyses apically spinulose; ascospores with completely thin walls and septa, I–; isidia usually present ..... ***Acanthotrema***
- Paraphyses apically glabrous; ascospores usually with at least slightly thickened septa and often thickened walls, I– or I+ (sometimes weakly) blue-violett; isidia absent in species treated here 17

17. Excipulum concentrically layered and fissured-lobulate, at least apically carbonized ..... ***Schizotrema***
- Excipulum simple, entire to undulate or fissured, rarely concentrically layered, uncarbonized 18

18. Apothecia with thallus and proper margin fissured-lobulate to recurved (chroodiscoid); excipulum usually fused with thallus margin, rarely free ..... ***Chapsa***
- Apothecia with thallus margin entire and proper margin undulate to slightly fissured; excipulum free, forming conspicuous double margin ..... ***Thelotrema***

19. Excipulum at least apically carbonized 20
- Excipulum colorless to (dark) brown but not carbonized 22

20. Hymenium inspersed; protocetraric acid present except in one species; disc often pigmented ..... ***Ampliotrema* p.p.**
- Hymenium not inspersed; protocetraric acid absent; disc not pigmented but medulla sometimes pigmented 21

21. Ascospores I– (non-amyloid) ..... ***Clandestinotrema* (*erumpens*)**
- Ascospores I+ violet-blue ..... ***Ocellularia* p.p.**

22. Ascospores colorless 23
- Ascospores brown 28

23. Ascospores I– (non-amyloid); stictic or norstictic acid or no substances; ascospores up to 50 µm long 24
- Ascospores I+ violet-blue; psoromic, protocetraric, or hypoprotocetraric acid or no substances, if stictic acid then ascospores over 50 µm long 25

24. Thallus cortex loose, surface opaque ..... ***Leucodecton* (*expallescens*)**
- Thallus cortex dense and splitting, surface glossy ..... ***Wirthiotrema* p.p.**

25. Excipulum apically with projecting fibrils; psoromic acid (medulla P+ yellow) ..... ***Fibrillithecis***
- Excipulum lacking fibrils; chemistry variable 26

26. Secondary substances absent; apothecia myriotremoid, with narrow pore and brown-black margin; excipulum fused; ascospores colorless, submuriform ..... ***Pycnotrema* (*pycnoporellum*)**
- Secondary substances usually present (medulla P+ yellow or orange or section with K+ yellow efflux), if absent then either excipulum free or ascospores transversely septate; if apothecia myriotremoid then with pale to white margin 27

27. Apothecia usually immersed, with narrow pore; excipulum colorless to pale brown ..... ***Myriotrema* p.p.**
- Apothecia usually erumpent to prominent, with narrow to wide pore; excipulum pale to dark brown ..... ***Ocellularia* p.p.**

28. Stictic or norstictic acid 29
- Chemistry variable but stictic and norstictic acids absent 30

29. Thallus cortex loose, surface opaque ..... ***Leucodecton***
- Thallus cortex dense and splitting, surface glossy ..... ***Wirthiotrema* p.p.**

30. Apothecia large, thallus and proper margin fissured-lobulate to recurved (chroodiscoid); isidia usually present ..... ***Reimnitzia* (*santensis*)**
- Apothecia variable but not large and chroodiscoid; isidia absent 31

31. Spotlike clusters of red crystals in photobiont layer and medulla ..... ***Leptotrema (wightii)***
- No clusters of red crystals present 32

32. Apothecia usually immersed, with narrow pore; excipulum colorless to pale brown ..... ***Myriotrema* p.p.**
- Apothecia usually erumpent to prominent, with narrow to wide pore; excipulum pale to dark brown ..... ***Ocellularia* p.p.**

33. Soralia present 34
- Isidia or schizidia present 36

34. Soralia large, capitate, strongly contrasting with the dark green thallus; stictic acid ..... ***Chapsa* (*thallotrema*)**
- Soralia small or irregular-effuse; psoromic acid or no substances 35

35. Soralia irregular-effuse; thallus light olive; psoromic acid ..... ***Myriotrema* (*pulverulentum*)**
- Soralia distinct; thallus dark olive; no substances ..... ***Chapsa* (*defectosorediata*)**

36. Schizidia present 37
- Isidia present 39

37. Schizidia disc-like, produced on top of large thallus warts; psoromic acid ..... ***Stegobolus* (*berkeleyanus*)**
- Schizidia irregular or if disc-like, then produced directly on thallus surface; stictic or hypoprotocetraric acid and lichexanthone 38

38. Schizidia disc-like; stictic acid ..... ***Myriotrema* (*frondosolucens*)**
- Schizidia irregular; hypoprotocetraric acid ..... ***Myriotrema* (*neofrondosum*)**

39. No substances 40
- Psoromic, protocetraric, or stictic acid 41

40. Thallus gall-forming, minutely grainy due to columnar clusters of calcium oxalate crystals, ecorticate, grey ..... ***Reimnitzia* (*santensis*)**
- Thallus not gall-forming, smooth, with dense cortex, olive ..... ***Acanthotrema* (*brasilianum, kalbii*)**

41. Isidia coarse; protocetraric or stictic acid 42
- Isidia delicate; psoromic acid 43

42. Stictic acid ..... ***Leucodecton* (*dactyliferum*)**
- Protocetraric acid ..... ***Ampliotrema* (*dactylizum*)**

43. Thallus olive; isidia sparse ..... ***Stegobolus* (*isidiiferus*)**
- Thallus white-grey; isidia dense 44

44. Isidia erect, with dark tip ..... ***Fibrillithecis* (*confusa*)**
- Isidia procumbent, with pale tip ..... ***Myriotrema* (*hartii*)**

Acanthotrema Frisch

Acanthotrema Frisch, Biblioth. Lichenol. 92: 77 (2006). Type. *Acanthotrema brasilianum* (Hale) Frisch.

Thallus grey-olive, with dense, partly splitting, prosoplectenchymatous cortex. Apothecia erumpent, angular-rounded to lobate (chroodiscoid); disc exposed; margin lobulate, fused. Columella absent. Excipulum paraplectenchymatous, uncarbonized; periphysoids present, apically spinulose. Paraphyses unbranched, apically spinulose. Ascospores septate to muriform, fusiform to ellipsoid, with thin septa and rectangular lumina, I– (non-amyloid). Secondary chemistry: no substances.

Remarks:—*Acanthotrema* is characterized by its chroodiscoid apothecia, but differs from other genera with similar apothecia by its spinulose paraphyses and periphysoids (Frisch 2006). In addition, and contrary to most other genera in the family, the ascospores are genuinely thin-walled. The only other genus with such ascospores, *Chroodiscus*, lacks periphysoids, has apically smooth paraphyses, and is exclusively foliicolous. Some species of *Chapsa*, such as *C. astroidea*, can be confused with *Acanthotrema* due to their similar apothecia and often almost thin-walled, non-amyloid ascospores, but these taxa always have apically smooth paraphyses. Species of *Acanthotrema* are typically found in lowland to montane rain forests. Two species were previously recognized (Rivas Plata *et al.* 2010a) and another two are described as new below.

Key to the species of *Acanthotrema* found in Costa Rica (3)

1. Ascospores 1-septate, 4–6 × 2–4 µm; thallus endoperidermal, reduced; isidia absent ..... ***A. bicellulare***
- Ascospores 3-septate to submuriform, 8–20 × 4–8 µm; thallus epiperidermal, well-developed; isidia usually present 2

2. Ascospores 3-septate, 8–14 × 4–6 µm ..... ***A. brasilianum***
- Ascospores (sub-)muriform, with 3–5 transverse and 0–1 longitudinal septa per segment, 14–20 × 6–8 µm ..... ***A. kalbii***

Acanthotrema bicellulare Sipman & Lücking, *spec. nov.* (Fig. 5A)

MycoBank #800069

Chapsa bicellularis Sipman & Lücking in Rivas Plata *et al.*, Lichenologist 42: 153 (2010); nom. inval. *Differing from other species of Acanthotrema in the endoperidermal thallus and small, 1-septate ascospores.*

Holotype:—COSTA RICA: Puntarenas: Carara National Park (Pacífico Central Conservation area), 84° 35' W, 9° 47' N, 100 m; lowland moist forest zone, partly disturbed primary forest along stream with dense *Erythrochiton gymnanthus* understory, on bark (stem) in clearing, July 2002, *Sipman 48392a* (INB-0003987219; isotype: B).

Thallus light yellowish white, smooth to uneven, ecorticate, endoperidermal; photobiont layer with scattered clusters of calcium oxalate crystals. Apothecia immersed, angular-rounded, 0.2–0.5 mm diam.; disc exposed, flesh-colored to pale brown; margin lobulate to recurved, fused, pale brown. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present, distinct. Hymenium 40–50 µm high, clear; paraphyses unbranched, apically spinulose. Ascospores 8/ascus, 1-septate, 4–6 × 2–3 µm, ellipsoid, with thin septa and rectangular lumina, colorless, I–. Secondary chemistry: no substances detected by TLC.

Remarks:—This species is easily recognized by its small, bicellular spores. It looks different from the other species of the genus because the thallus is reduced and endoperidermal and the apothecia are smaller. Several species of *Chapsa* have a similar morphology and we first intended to describe this species in that genus (Rivas Plata *et al.* 2010a), but because of the spinulose paraphyses and thin-walled, *Chroodiscus*-type ascospores, we have placed this new taxon in *Acanthotrema*. It appears to be a lowland rain forest species.

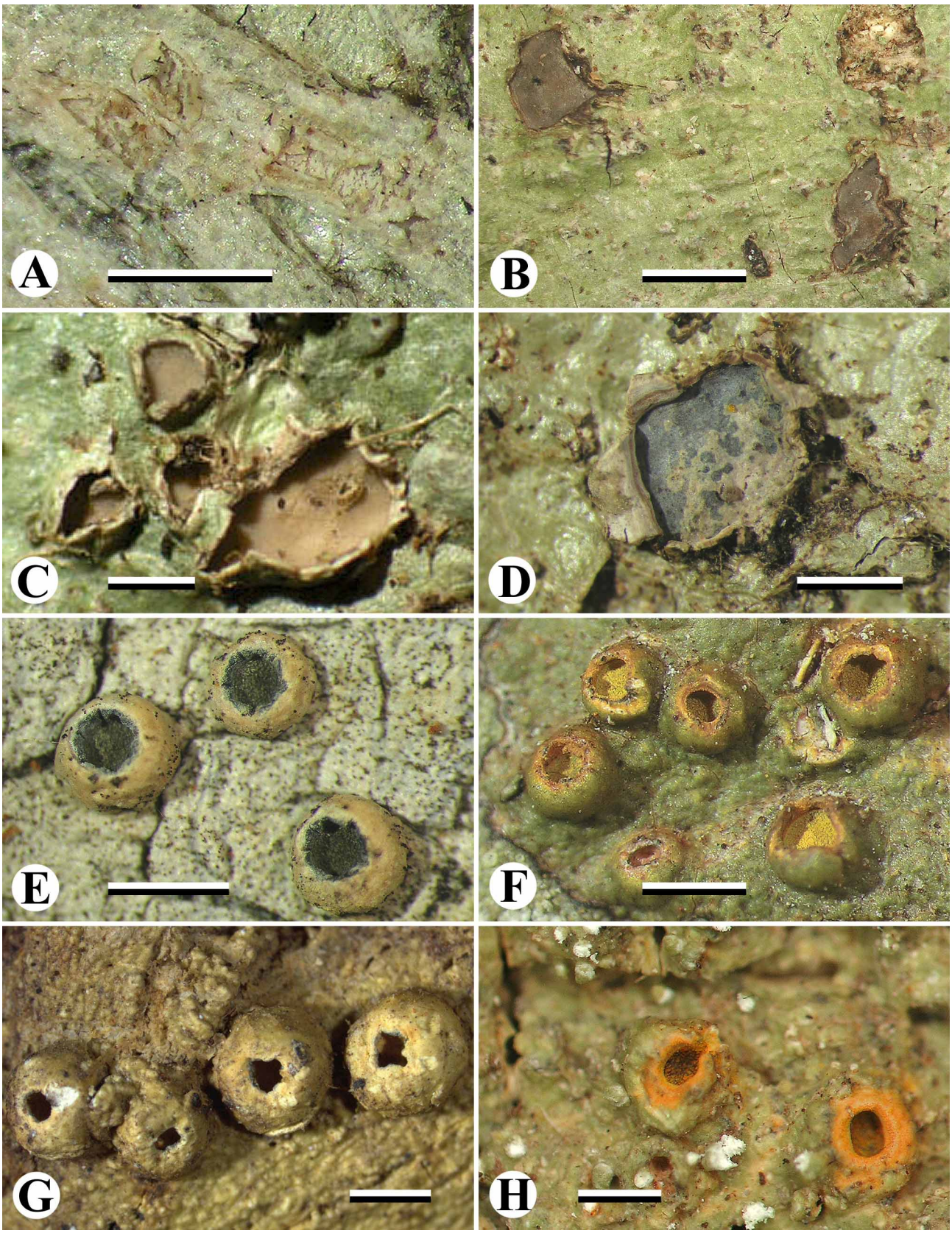

FIGURE 5. A. *Acanthotrema bicellularis*. B–C. *Acanthotrema brasilianum*. D. *Acanthotrema kalbii*. E. *Ampliotrema amplius*. F. *Ampliotrema auratum*. G. *Ampliotrema cocosense*. H. *Ampliotrema dactylizum*. Scale = 1 mm.

Additional specimen examined (paratype):—COSTA RICA. Puntarenas: Carara National Park, Quebrada Bonita Section (Pacífico Central Conservation Area), 60 km WSW of San Jose on road from Orotina to Quepos (34), trail from visitor's center to Quebrada Bonita; 84° 35' W, 9° 47' N, 100 m; lowland moist forest zone, partly disturbed dense primary forest with understory dominated by *Erythrochiton gymnanthus*, on bark (lower stem), partially shaded; July 2002, *Lücking 15629b* (F).

***Acanthotrema brasilianum* (Hale) Frisch** (Fig. 3N, 5B–C)

Acanthotrema brasilianum (Hale) Frisch, Biblioth. Lichenol. 92: 78 (2006); *Thelotrema brasilianum* Hale in Kalb, Lich. Neotrop. Fasc. VII: 15 (1983). Holotype. Brazil, *Malme 3588* (S!).
Thelotrema carneoradians Sipman, Trop. Bryol. 6: 10 (1992). Holotype. Venezuela, *Sipman 26355* (VEN!; isotype: B!).

Thallus grey-green, smooth to uneven, producing up to 2 mm long, slender isidia, with dense, partly splitting, prosoplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded to lobate, 1–2.5 mm diam.; disc exposed, flesh-colored to pink-purple; margin lobulate, fused, lobules erect to recurved, pale grey-brown. Columella absent. Excipulum paraplectenchymatous, pale brown; periphysoids present, distinct, apically spinulose. Hymenium 50–70 µm high, clear; paraphyses unbranched, apically spinulose. Ascospores 8/ascus, 3-septate, 8–14 × 4–6 µm, fusiform to narrowly ellipsoid, with thin septa and rectangular lumina, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Acanthotrema brasilianum* is the most common and widespread of the three species currently distinguished. The African *A. frischii*, which was previously confused with *A. brasilianum* (Frisch 2006), has broadly oval, always submuriform ascospores (Rivas Plata *et al.* 2010a). The newly described *A. kalbii* has ascospores similar to those of *A. brasilianum* in shape but they are distinctly larger and (sub-)muriform. *Acanthotrema brasilianum* should not be confused with *Chapsa astroidea*, which looks superficially similar but has apically smooth paraphyses and slightly larger ascospores with 3–5 septa. Based on molecular data, the two species are not closely related, in spite of their similarities (Rivas Plata *et al.* 2012a, b). *Acanthotrema brasilianum* occurs in lowland to montane rain forest on tree trunks in the shaded understory.

Specimens examined:—COSTA RICA. Alajuela: Maquenque Mixed National Wildlife Refuge, Huetar Norte; 84° 11' W, 10° 42' N, 0–100 m; Apr 2005, *Chaves 2351*, *2360* (INB). Cartago: Cerros de La Carpintera Protection Zone, Cordillera Volcánica Central; 1700–1800 m; Aug 2008; *Chaves 3220* (INB). Limón: Veragua, La Amistad Caribe, Los Valientes trail; 200–300 m; Jun 2009, *Chaves 3819* (INB). Puntarenas: San Vito de Coto Brus, Las Cruces Biological Station; 82° 58' W, 8° 47' N, 1200 m; on ridge beyond Río Java, on trunks and undergrowth of disturbed primary forest; Oct 2004, *Sipman 53247* (B, INB).

Acanthotrema kalbii* Lücking, *spec. nov. (Fig. 5D)
MycoBank #800070

Differing from *Acanthotrema brasilianum* in the larger, regularly submuriform ascospores.

Holotype:—COSTA RICA. Puntarenas: Las Tablas Protection Zone, Cedro Ridge, Las Alturas Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km NE of San Vito near Alturas, surroundings of station and trail into forest; 82° 50' W, 8° 57' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower stem), partially shaded; Jun 2002, *Lücking 15070b* (F).

Thallus grey-green, smooth to uneven, producing up to 2 mm long, slender isidia, with dense, partly splitting, prosoplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded to lobate, 1–2 mm diam.; disc exposed, grey-purple; margin

lobulate, fused, lobules erect to recurved, pale grey-brown. Columella absent. Excipulum paraplectenchymatous, pale brown; periphysoids present, distinct, apically spinulose. Hymenium 60–80 µm high, clear; paraphyses unbranched, apically spinulose. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–1 longitudinal septa per segment, 14–20 × 6–8 µm, fusiform to narrowly ellipsoid, with thin septa and rectangular lumina, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Acanthotrema brasilianum* has been circumscribed as having 3-septate ascospores intermingled with submuriform ones (Kalb 1983; Staiger & Kalb 1999; Staiger 2002; Frisch 2006). Revision of the known collections showed that the African populations have a different ascospore type (broadly oval) and thus represent a distinct species (Rivas Plata *et al.* 2010a). All Neotropical collections have fusiform to narrowly ellipsoid ascospores. Material from the Amazon consistently has small, 3-septate ascospores, whereas in the populations from the southern Atlantic rain forest in Brazil, ascospores with single longitudinal septa occasionally occur. The material from Costa Rica can clearly be divided into two forms: with small, 3-septate ascospores and with distinctly larger (sub-)muriform ascospores. The latter are also larger than those found in southern Brazil and therefore this material is here regarded as taxonomically distinct. *Acanthotrema kalbii* is dedicated to our esteemed colleague and friend, Klaus Kalb, for his substantial and invaluable contributions to tropical lichenology.

Ampliotrema Kalb ex Kalb

Ampliotrema Kalb, Biblioth. Lichenol. 88: 301 (2004); Kalb in Frisch, Biblioth. Lichenol. 92: 81 (2006). Type. *Ampliotrema amplius* (Nyl.) Kalb.

Thallus with dense, proso- to usually paraplectenchymatous cortex. Apothecia prominent to sessile, rounded; disc partially covered by wide pore, white- to grey- or yellow- to red-pruinose; margin entire, fused. Columella absent. Excipulum paraplectenchymatous, carbonized; periphysoids absent. Paraphyses apically branched; hymenium inspersed. Ascospores septate to muriform, ellipsoid to oblong-cylindrical, with thick septa and rounded lumina, colorless or rarely brown, I+ violet-blue (amyloid). Secondary chemistry: mostly protocetraric and virensic acids, apothecial disc often with yellow to red anthraquinones.

Remarks:—*Ampliotrema* belongs in the large *Ocellularia-Myriotrema* clade and shares the amyloid ascospores with thick septa and rounded lumina, as well as the absence of periphysoids, with all other representatives of this clade (Rivas Plata *et al.* 2012b). *Ampliotrema* species are very uniform in always having prominent to sessile apothecia with comparatively wide pore, a carbonized excipulum (paraplectenchymatous in thin sections), no columella, an inspersed hymenium, and the protocetraric acid chemosyndrome. No other species in the family have this combination of characters. Most similar in appearance are species of the *Ocellularia bahiana* group, namely *O. bahiana* itself, which closely resembles *Ampliotrema* in morphology and chemistry but has a uncarbonized excipulum and non-inspersed hymenium. *Ampliotrema* was recognized as separate genus by Frisch (2006) but not by Mangold *et al.* (2009); it appears to be nested within *Ocellularia* s.lat. (Mangold *et al.* 2008a; Rivas Plata *et al.* 2012b). However, more data are needed before the generic concepts within that clade can be settled. We therefore follow the view of Frisch (2006) and maintain *Ampliotrema* separate from *Ocellularia*. Several species of *Ampliotrema* have conspicuous apothecia due to the vividly pigmented discs.

Key to the species of *Ampliotrema* found or expected in Costa Rica (9)

1. Ascospores transversely septate; apothecial disc variously colored 2
- Ascospores (sub-)muriform; apothecial disc yellow-orange pruinose 6

2. Ascospores small, 20–30 µm long, 5–9-septate 3

- Ascospores medium-sized to large, 50–150 µm long, 11–35-septate 4

3. Apothecial disc grey-pruinose ..... ***A. amplius***
- Apothecial disc orange-pruinose ..... ***A. discolor***

4. Apothecial disc grey-pruinose ..... ***A. palaeoamplius***
- Apothecial disc orange-pruinose 5

5. Thallus with coarse isidia that easily break off; ascospores 50–90 µm long..... ***A. dactylizum***
- Thallus lacking isidia; ascospores 60–150 µm long ..... ***A. lepadinoides***

6. Ascospores large, 80–100 × 17–22 µm ..... ***A. cocosense***
- Ascospores small, 14–30 × 8–12 µm..... 7

7. Ascospores colorless; disc partially covered by wide pore ..... ***A. auratum***
- Ascospores brown; disc covered by narrow pore 8

8. Protocetraric acid (medulla P+ orange-red)..... ***A. panamense***
- No substances (medulla P–)..... ***A.* aff. *panamense***

***Ampliotrema amplius* (Nyl.) Kalb** (Fig. 5E)

Ampliotrema amplius (Nyl.) Kalb in Frisch, Biblioth. Lichenol. 92: 81 (2006); Kalb, Biblioth. Lichenol. 88: 302 (2004); *Thelotrema cavatum* var. *amplius* Nyl., Ann. Sci. Nat. Bot., Sér. 5, 7: 316 (1867); *Ocellularia amplior* (Nyl.) Redinger, Arkiv Bot. 28A(8): 16 (1936). Holotype. Colombia, *Lindig 99* (H-Nyl. 22831!; isotype: M!).

Thallus grey-olive, smooth to uneven, with dense, proso- to paraplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia sessile, rounded, 0.6–1 mm diam.; disc partially covered by up to 0.4 mm wide pore, grey-pruinose; margin entire, fused, brown-black, covered by thalline layer. Columella absent. Excipulum paraplectenchymatous, carbonized; periphysoids absent. Hymenium 100–120 µm high, inspersed; paraphyses apically branched. Ascospores 8/ascus, 5–9-septate, 15–25 × 8–10 µm, ellipsoid, with thick septa and rounded lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: protocetraric and virensic acids (exposed medulla P+ orange-red; section K–).

Remarks:—*Ampliotrema amplius* belongs to a group of species with non-pigmented, grey-pruinose apothecial discs. Among these, it is characterized by small, transversely septate ascospores. The closely related *A. palaeoamplius* (see below) has much longer spores, whereas they are large and muriform in *A. cocosense* (see below). *Ampliotrema amplius* is a lowland to montane rain forest species, preferring semi-exposed situations.

Specimens examined:—COSTA RICA. Alajuela: San Ramón Forest Reserve, near house at Río Lorencito, 5 km NE of Cerro Jabonal; 84° 37' W, 10° 13' N, 1000 m; humid, mossy forest with many ferns on mountain ridge, on thin trunk in undergrowth; Nov 1988, *Sipman et al. 41993* (B, CR). Puntarenas: Corcovado National Park, Los Patos Section, Los Patos Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, access trail to station and first, hilly part (5 km) of trail to Sirena; 83° 29' W, 8° 34' N, 100–300 m; lowland rain forest zone, closed primary forest, on bark (upper trunk), exposed; Apr 2003, *Lücking 16300a* (F, INB). Las Tablas Protection Zone, La Neblina Section (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km ENE of San Vito near Las Mellizas, access road to fincas; 82° 45' W, 8° 55' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower trunk), semi-exposed; Jun 2002, *Lücking 15114a* (F).

***Ampliotrema auratum* (Tuck.) Kalb** (Fig. 5F)

Ampliotrema auratum (Tuck.) Kalb in Frisch, Biblioth. Lichenol. 92: 82 (2006); Kalb, Biblioth. Lichenol. 88: 302 (2004); *Thelotrema auratum* Tuck., Proc. Amer. Acad. Arts Sci. 5: 408 (1862). Lectotype (Hale 1978: 41). Cuba, *Wright s.n.* (FH!; Lichenes Cubae 133).
Thelotrema citrinodiscus Redinger, Arkiv Bot. 28A(8): 77 (1936). Lectotype (Hale 1978: 41). Brazil, *Malme 88* (S!).

Thallus grey-olive, smooth to uneven, with dense, proso- to paraplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia sessile, rounded, 1–1.3 mm diam.; disc partially covered by up to 0.6 mm wide pore, yellow-pruinose; margin entire, fused, brown-black, covered by thalline layer. Columella absent. Excipulum paraplectenchymatous, carbonized; periphysoids absent. Hymenium 100–120 µm high, inspersed; paraphyses apically branched. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–1 longitudinal septa per segment, 15–25 × 8–12 µm, ellipsoid, with thick septa and rounded lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: protocetraric and virensic acids (exposed medulla P+ orange-red; section K–), apothecial disc with yellow (K+ red) pigment.

Remarks:—This species combines the characters of a yellow-pigmented apothecial disc with small, submuriform ascospores. Hale (1978) and subsequent authors (Frisch 2006; Mangold *et al.* 2009) united under *A. auratum* the paleotropical *Thelotrema oculatum* Vain. and *T. porphyrodiscus* Zahlbr., which have differently colored apothecial pigments (cinnabar-red and purple-red, respectively). Since the differences in apothecial color are constant and correlate with geographic distribution, we favor the recognition of different species involved in this complex; for example, the yellow *auratum* type appears to be restricted to the Neotropics whereas all Australian collections conform to the cinnabar-red *oculatum* type. Most similar to *A. auratum* is *A. panamense* (see below), which has brown ascospores and a narrow pore covering the apothecial disc.

Specimens examined:—Not yet found in Costa Rica but reported from Panama (Hale 1978).

***Ampliotrema cocosense* Lücking & Chaves** (Fig. 5G)

Ampliotrema cocosense Lücking & Chaves in Lumbsch *et al.*, Phytotaxa 18: 14 (2011). Holotype: Costa Rica, *Lücking s.n.* (CR!; isotypes: F!, INB!, USJ!).

Thallus grey-olive-yellow, verrucose, with dense, paraplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia sessile, rounded, 1–2 mm diam.; disc partially covered by 0.3–0.6 mm wide pore, brown-black, yellow-orange-pruinose; margin entire, fused, yellowish white, covered by thalline layer. Columella absent. Excipulum paraplectenchymatous, carbonized; periphysoids absent. Hymenium 150–200 µm high, inspersed; paraphyses apically branched. Ascospores 4–8/ascus, richly muriform, 80–100 × 17–22 µm, oblong, with thick septa and rounded lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: protocetraric and virensic acids (exposed medulla P+ orange-red; section K–), apothecial disc with yellow-orange (K+ red) pigment.

Remarks:—*Ampliotrema cocosense* is known from one well-developed collection made on Cocos Island (Lumbsch *et al.* 2011). The lichens of this island are not well-known except for the foliicolous species (Dodge 1935; Weber 1993; Lücking & Lücking 1995), and the fact that the only two thelotremoid Graphidaceae collected there are new to science (see below under *Ocellularia cocosensis*) indicates that for certain groups, Cocos Island harbours a unique lichen biota. *Ampliotrema cocosense* is the only species in the genus with large, muriform ascospores, and hence it easy to recognize. From species of *Ocellularia* s.lat. with similar ascospores, it is set apart by the combination of a wide pore with pigmented disc, absence of columella, paraplectenchymatous excipulum, inspersed hymenium, and protocetraric acid as the main secondary substance.

Ampliotrema dactylizum* (Hale) Sipman, Lücking & Grube, *comb. nov. (Fig. 5H)
MycoBank #800058

Ocellularia dactyliza Hale, Smithson. Contr. Bot. 38: 19 (1978). Holotype. Panama, *Hale 43559* (US!).
Ocellularia auratipruinosa Breuss, Linzer Biol. Beitr. 32: 1047 (2000). Holotype. Costa Rica, *Breuss 15817* (LI!).

Thallus grey-olive, verrucose, producing coarse isidia up to 1 mm long that easily break and leave behind white spots (medulla), with dense, proso- to paraplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.7–1.5 mm diam.; disc covered by 0.2–0.5 mm wide pore; margin entire, fused, brown-black, covered by thalline layer. Columella absent. Excipulum paraplectenchymatous (apically) carbonized; periphysoids absent. Hymenium 180–220 µm high, inspersed; paraphyses apically branched. Ascospores 4–8/ascus, 11–19-septate, 50–90 × 10–14 µm, oblong, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: protocetraric and virensic acids (exposed medulla P+ orange-red; section K–), apothecial disc with orange (K+ red-purple) pigment.

Remarks:—*Ampliotrema dactylizum* is close to *A. lepadinoides* (see below) in apothecial morphology and ascospores, but differs clearly in the coarsely isidiate thallus; also, the ascospores are shorter compared to the latter species. The species was described as *Ocellularia auratipruinosa* from Costa Rica (Breuss 2000), but revision of the type of *Ocellularia dactyliza* revealed conspecifity of both taxa; the material of the latter has mostly young apothecia but the orange disc and coarse isidia were easily observed. The isidia often break off and leave behind white dots that resemble tiny, young soralia. This species was only found on shaded tree trunks in lowland rain forest.

Specimens examined:—COSTA RICA. Puntarenas: Corcovado National Park, Los Patos Section, Los Patos Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, access trail to station and first, hilly part (5 km) of trail to Sirena; 83° 29' W, 8° 34' N, 100–300 m; lowland rain forest zone, closed primary forest, on bark (lower trunk), partially shaded; Apr 2003, *Grube 11455* (GZU, INB).

***Ampliotrema discolor* (Ach.) Kalb** (Fig. 6A)

Ampliotrema discolor (Ach.) Kalb in Frisch, Biblioth. Lichenol. 92: 81 (2006); Kalb, Biblioth. Lichenol. 88: 303 (2004); *Pyrenula discolor* Ach., Ges. Naturf. Freunde Berlin Mag. 6: 9 (1814); *Ocellularia discolor* (Ach.) Spreng. in Meyer, Entw. Flecht.: 328 (1824); *Thelotrema discolor* (Ach.) Vain., Ann. Acad. Sci. Fenn., Ser. A, 6(7): 140 (1915). Lectotype (Nylander 1867: 552). America, s.col. (UPS!; isolectotype: H-ACH 804!).

Thallus grey-olive, smooth to uneven, with dense, paraplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia sessile, rounded, 0.8–1.5 mm diam.; disc partially covered by 0.3–0.5 mm wide pore, brown-black, orange-pruinose; margin entire, fused, brown-black, covered by thalline layer. Columella absent. Excipulum paraplectenchymatous, carbonized; periphysoids absent. Hymenium 90–120 µm high, inspersed; paraphyses apically branched. Ascospores 8/ascus, 5–9-septate, 20–30 × 8–10 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: protocetraric and virensic acids (exposed medulla P+ orange-red; section K–), apothecial disc with orange (K+ red-purple) pigment.

Remarks:—This species can be distinguished from the similar *Ampliotrema lepadinoides* (see below) by the much smaller ascospores. *Ampliotrema amplius* (see above) has the same ascospore type but lacks the orange apothecial pigment. As already stated by Hale (1972), Matsumoto (2000), and Kalb (2004), the type material of *Pyrenula discolor* is heterogeneous and includes also the columellate species *Ocellularia cinchonarum*. Hale (1972) selected the latter as lectotype, which was corrected by Matsumoto (2000) and Kalb (2004), since Nylander (1867: 320) had already excluded this explicitedly by stating "...*immixtum cum Ascidio cinchonarum*".

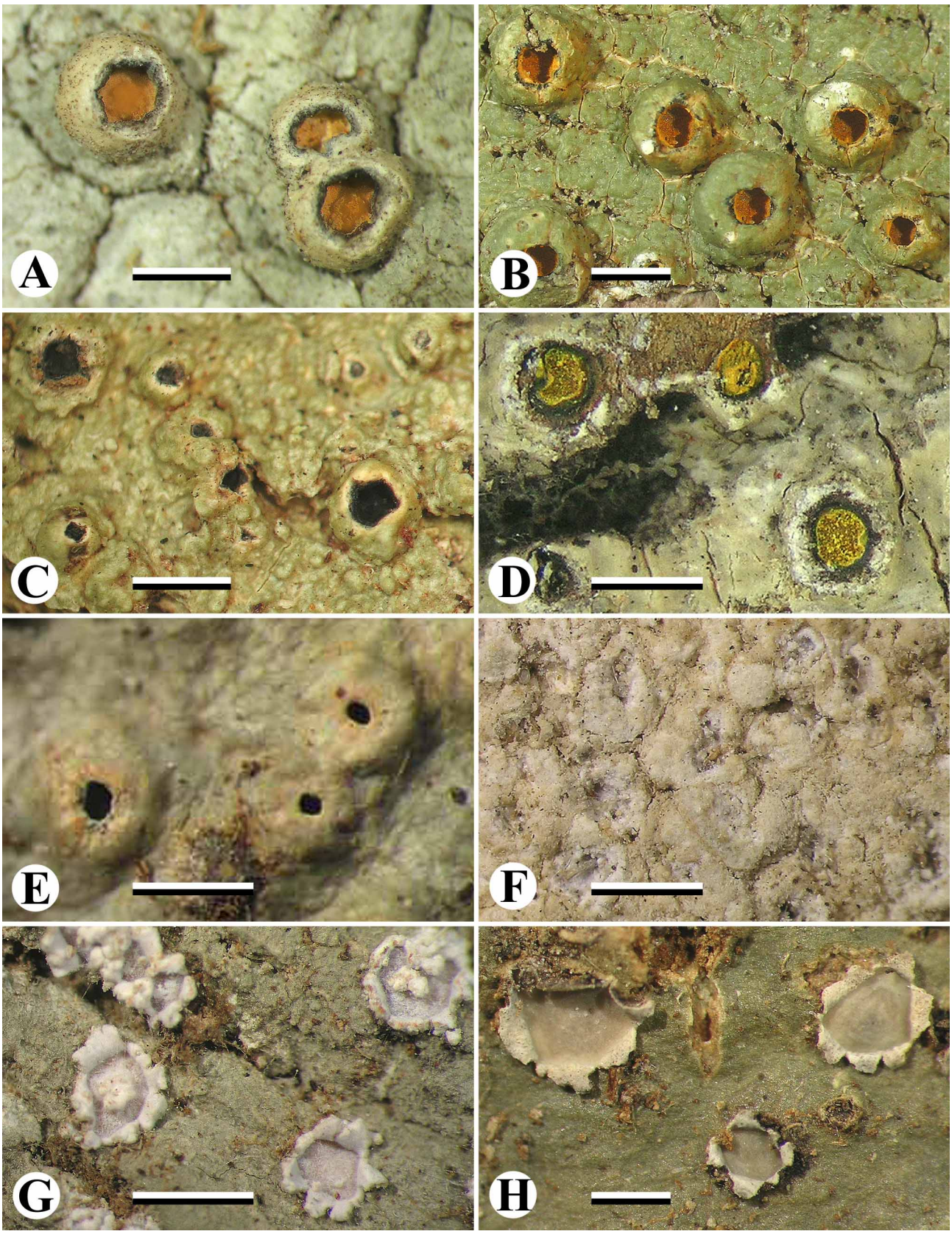

FIGURE 6. A. *Ampliotrema discolor*. B. *Ampliotrema lepadinoides*. C. *Ampliotrema palaeoamplius*. D. *Ampliotrema panamense*. E. *Ampliotrema* aff. *panamense*. F. *Chapsa albida*. G. *Chapsa alborosella*. H. *Chapsa astroidea*. Scale = 1 mm.

Specimens examined:—COSTA RICA. Puntarenas: Corcovado National Park, Los Patos Section, Los Patos Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, access trail to station and first, hilly part (5 km) of trail to Sirena; 83° 29' W, 8° 34' N, 100–300 m; lowland rain forest zone, closed primary forest, on bark (branch, fallen), exposed; Apr 2003, *Lücking 16309g* (F, INB).

***Ampliotrema lepadinoides* (Leight.) Kalb** (Fig. 6B)

Ampliotrema lepadinoides (Leight.) Kalb in Frisch, Biblioth. Lichenol. 92: 81 (2006); Kalb, Biblioth. Lichenol. 88: 303 (2004); *Thelotrema lepadinoides* Leight., Trans. Linn. Soc. London 25: 447 (1866); *Ocellularia lepadinoides* (Leight). Zahlbr., Cat. Lich. Univ. 2: 594 (1923). Holotype. Brazil, *Spruce 245* (BM!; isotype: H-NYL 22812!).

Thallus grey-olive, smooth to uneven, with dense, proso- to paraplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia sessile, rounded, 1–2 mm diam.; disc partially covered by 0.3–0.6 mm wide pore, brown-black, orange-pruinose; margin entire, fused, brown-black, covered by thalline layer. Columella absent. Excipulum paraplectenchymatous, carbonized; periphysoids absent. Hymenium 150–230 µm high, inspersed; paraphyses apically branched. Ascospores 8/ascus, 60–150 × 10–12 µm, cylindrical, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid), 15–35-septate. Secondary chemistry: protocetraric and virensic acids (exposed medulla P+ orange-red; section K–), apothecial disc with orange (K+ red-purple) pigment.

Remarks:—The large, multiseptate ascospores in combination with the orange apothecial pigment set this species apart from all others in the genus. The most closely related *Ampliotrema dactylizum* (see above) has a coarsely isidiate thallus and slightly shorter ascospores. *Ampliotrema lepadinoides* was found on shaded tree trunks in lowland rain forest.

Specimens examined:—COSTA RICA. Puntarenas: Corcovado National Park, Los Patos Section, Los Patos Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, access trail to station and first, hilly part (5 km) of trail to Sirena; 83° 29' W, 8° 34' N, 100–300 m; lowland rain forest zone, closed primary forest, on bark (lower trunk), partially shaded; Apr 2003, *Grube 11446* (GZU, INB), *Lücking 16311b* (CR, F, INB, USJ). Finca Quebrada Bonita-Garabú, La Fila; 83° 35' W, 9° 34' N, 0–100 m; Nov 2008, *Chaves 3330* (INB).

***Ampliotrema palaeoamplius* (Aptroot & Sipman) Kalb** (Fig. 6C)

Ampliotrema palaeoamplius (Aptroot & Sipman) Kalb in Frisch, Biblioth. Lichenol. 92: 81 (2006); Kalb, Biblioth. Lichenol. 88: 303 (2004); *Ocellularia palaeoamplior* Aptroot & Sipman, J. Hattori Bot. Lab. 91: 333 (2001). Holotype. China (Hong Kong), *Sipman 45124* (= *Aptroot 48628*) (B!; isotypes: F!, HKU-M).

Thallus grey-olive, uneven-verrucose, with dense, proso- to paraplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia sessile, rounded, 0.6–1 mm diam.; disc partially covered by up to 0.4 mm wide pore, grey-pruinose; margin entire, fused, brown-black, covered by thalline layer. Columella absent. Excipulum paraplectenchymatous (upper half) carbonized; periphysoids absent. Hymenium 150–200 µm high, inspersed; paraphyses apically branched. Ascospores 4–6/ascus, 13–21-septate, 50–80 × 8–13 µm, oblong, with thick septa and rounded lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: protocetraric and virensic acids (exposed medulla P+ orange-red; section K–).

Remarks:—This species is most similar to *Ampliotrema amplius* (see above) but differs clearly in the much longer ascospores with more numerous septa. The thallus of *A. palaeoamplius* is also typically verrucose. The ascospores resemble those of *A. dactylizum* and *A. lepadinoides* (see above), which differ in their orange apothecial discs. The type material of *Ocellularia palaeoamplior* was cited as both *Sipman 15124*

and *Aptroot 48628* in the protologue (Aptroot & Sipman 2001, Frisch 2006). The correct number is *Sipman 45124* and in order to avoid nomenclatural problems, both collectors and numbers have been annotated on each specimen..

Specimens examined:—COSTA RICA. Puntarenas: Corcovado National Park, Los Patos Section, Los Patos Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, access trail to station and first, hilly part (5 km) of trail to Sirena; 83° 29' W, 8° 34' N, 100–300 m; lowland rain forest zone, closed primary forest, on bark (lower trunk), semi-exposed; Apr 2003, *Nelsen 3567e* (INB, WIS).

Ampliotrema panamense* (Hale) Sipman & Lücking**, ***comb. nov. (Fig. 6D)
MycoBank #800055

Leptotrema panamense Hale, Smithson. Contr. Bot. 38: 54 (1978); *Ocellularia panamensis* (Hale) Hale, Mycotaxon 11: 137 (1980). Holotype. Panama, *Hale 43584* (US!).

Thallus light grey-olive, verrucose, with dense, proso- to paraplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia sessile, rounded, 0.7–1 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore; margin entire, fused, brown-black, covered by thalline layer. Columella absent. Excipulum prosoplectenchymatous, apically carbonized; periphysoids absent. Hymenium 100–130 µm high, inspersed; paraphyses apically branched. Ascospores 6–8/ascus, submuriform with 3–5 transverse septa and 0–1 longitudinal septa per segment, 24–28 × 10–12 µm, fusiform, with thick septa and rounded lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: protocetraric and virensic acids (exposed medulla P+ orange-red; section K–), apothecial disc with yellow (K+ red) pigment.

Remarks:—This is thus far the only species accepted in the genus with brown ascospores. This character and the narrow apothecial pore set it apart from the otherwise similar *A. auratum* (see above).

Specimens examined:—Not yet found in Costa Rica but reported from Panama (Hale 1978).

***Ampliotrema* aff. *panamense* (Hale) Sipman & Lücking** (Fig. 6E)

Remarks:—This material agrees with *Ampliotrema panamense* but TLC did not show any traces of secondary substances. We have detected another undescribed species of *Ampliotrema* lacking secondary substances in the thallus in Venezuela (Lücking *et al.*, unpubl. data) and therefore, also following our concepts used in other genera, we cannot simply assume that the present material is an acid-deficient specimen of *A. panamense*.

Specimens examined:—COSTA RICA. Guanacaste: Cacao Biological Station (Guanacaste Conservation Area); 10° 56' N, 85° 28' W, 1000 m; epiphyte in humid primary montane forest near the station; Jun 1995, *Sipman 37292* (B, CR).

Chapsa A. Massal.

Chapsa A. Massal., Atti Reale Ist. Veneto Sci. Lett. Arti, Ser. 3(5): 256 (1860); Frisch, Biblioth. Lichenol. 92: 84 (2006). Type. *Chapsa indica* A. Massal.

Thallus ecorticate or rarely with loose or dense, proso- to paraplectenchymatous cortex. Apothecia erumpent to rarely sessile, rounded to irregular lobate-lirelline; disc exposed or partially covered by excipular remnants; margin lobulate to recurved, fused or with split between excipulum and thalline margin. Columella absent. Excipulum paraplectenchymatous, uncarbonized; periphysoids present. Paraphyses unbranched,

apically often capitate or moniliform. Ascospores septate to muriform, fusiform-ellipsoid to oblong-cylindrical, with thin to thick septa and angular to rounded lumina, colorless or rarely brown, I– or I+ weakly to strongly violet-blue (amyloid). Secondary chemistry: no substances or frequently stictic acid and relatives.

Remarks:—The genus *Chapsa* was reintroduced by Frisch (2006) to accommodate the bulk of taxa with chroodiscoid apothecia, excluding *Acanthotrema* (paraphyses apically spinulose, ascospores thin-walled), *Chroodiscus* (foliicolous, periphysoids absent, ascospores thin-walled), and *Reimnitzia* (periphysoids absent, deviating ascus type, thallus with columnar crystal clusters). *Chapsa* is still a heterogeneous assemblage (Rivas Plata *et al.* 2010a) and at times difficult to separate from *Thelotrema* (apothecia lepadinoid with double margin) and *Topeliopsis* (apothecia usually with layered excipulum and incurved margins). Molecular phylogenetic analysis suggests that *Chapsa* represents at least two related but separate clades (Rivas Plata & Lumbsch 2011a, b), but no discriminating morphological characters appear to correlate with this topology.

Key to the species and varieties of *Chapsa* found or expected in Costa Rica (26)

1. Ascospores colorless 2
- Ascospores grey-brown when mature 25

2. Ascospores transversely septate 3
- Ascospores muriform 20

3. Hymenium inspersed; ascospores 20–25 × 6–8 µm, 5–7-septate ..... ***C. pseudoschizostoma***
- Hymenium clear; ascospores variable 4

4. Ascospores 50–150 µm long, 15–35-septate; thallus with dense, prosoplectenchymatous cortex; apothecial margin often layered 5
- Ascospores 10–45 µm long, 1–15-septate; thallus cortex variable or absent; apothecial margin usually not layered. 9

5. Soralia present 6
- Soralia absent 7

6. Soralia large, capitate, with finely granular soredia; stictic acid ..... ***C. thallotrema***
- Soralia small, punctiform, with coarsely granular soredia; no substances ..... ***C. defectosorediata***

7. No substances ..... ***C. defecta***
- Stictic acid 8

8. Apothecial disc flesh-coloured to light purple ..... ***C. sublilacina*** var. ***sublilacina***
- Apothecial disc blue ..... ***C. sublilacina*** var. ***cyanea***

9. Stictic acid 10
- No substances or hypoprotocetraric acid 12

10. Thallus white, ecorticate; apothecia thickly white-pruinose, with irregular erect lobules, often elongate .. ***C. dilatata***
- Thallus pale green-grey, indistinctly or loosely corticate; apothecia thinly white-pruinose, with regular lobules, more or less rounded to angular 11

11. Apothecia small (up to 0.8 mm diam.), usually aggregate ..... ***C. phlyctidioides***
- Apothecia larger (0.8–1.2 mm diam.), solitary ..... ***C. esslingeri***

12. Thallus with dense, prosoplectenchymatous cortex, olive-green to dark brown 13
- Thallus ecorticate or with loose (to rarely dense) cortex, white-grey to yellow-white or light grey-green 17

13. Apothecia chroodiscoid with regular, recurved lobules 14
- Apothecia opening with irregular splits and with irregular, erect to inclined lobules when mature 15

14. Thallus endoperidermal, yellow-olive to olive-brown, often hardly visible; apothecial margin white, disc distinctly white-pruinose and appearing blue-grey; ascospores 3–5-septate, 10–15 µm long ..... ***C. platycarpella***
- Thallus epiperidermal, olive-green, conspicuous; apothecial margin pale brown, disc flesh-colored and thinly white-pruinose; ascospores 3–7-septate, 10–20 µm long ..... ***C. astroidea***

15. Hypoprotocetraric acid; apothecial margin concentrically layered ..... ***C. referta***
- No substances; apothecial margin not layered 16

16. Ascospores with distinct endospore, I+ violet-blue ..... ***C. dissuta***
- Ascospores thin-walled, I– ..... ***C. lassae***

17. Thallus ecorticate, thickly farinose, yellow-white ..... ***C. farinosa***
- Thallus with loose (to dense) cortex or if ecorticate then compact and light grey-green 18

18. Thallus ecorticate, light green ..... ***C. alborosella***
- Thallus with loose to dense cortex, yellow-white to pale brown 19

19. Ascospores 20–35 µm long, 7–15-septate; thallus with loose cortex ..... ***C. albida***
- Ascospores 10–18 µm long, 3–5-septate; thallus with dense cortex ..... ***C. chionostoma***

20. Hymenium inspersed; apothecia sessile; over bryophytes ..... ***C. meridensis***
- Hymenium clear; apothecia immersed to erumpent; on bark 21

21. Ascospores 12–60 µm long, (2–)4–8 per ascus 22
- Ascospores 60–180 µm long, 1–2(–4) per ascus 23

22. Ascospores 12–15 × 6–7 µm, submuriform ..... ***C. hiata***
- Ascospores 30–60 × 10–20 µm, muriform ..... ***C. discoides***

23. Thallus ecorticate; apothecia more or less chroodiscoid with erect to recurved lobules; ascospores 60–110 µm long. ..... ***C. leprocarpa***
- Thallus with dense, prosoplectenchymatous cortex; apothecia opening with irregular splits or if not, the excipulum layered; ascospores (70–)100–180 µm long 24

24. Apothecia opening with irregular splits, solitary ..... ***C. perdissuta***
- Apothecia opening forming more or less regular lobules but excipulum layered ..... ***C. laceratula***

25. Ascospores muriform, large (100–120 × 20–30 µm) ..... ***C. stellata***
- Ascospores (1–)3–5-septate, small (10–16 × 4–6 µm) 26

26. Excipulum fused; apothecial margin felty-pruinose; no substances ..... ***C. leprieurii***
- Excipulum free, apothecia with distinct double margin; stictic acid 27

27. Apothecial disc dark-red to purple-brown; thallus white-grey, endoperidermal, ecorticate ..... ***C. neei***
- Apothecial disc grey-brown; thallus olive-green, epiperidermal, with prosoplectenchymatous cortex.. ***C. platycarpa***

***Chapsa albida* (Nyl.) Lücking & Sipman** (Fig. 6F)

Chapsa albida (Nyl.) Lücking & Sipman in Rivas Plata *et al.*, Lichenologist 42: 182 (2010); *Thelotrema albidum* Nyl., Acta Soc. Sci. Fenn. 7: 451 (1863); *Ocellularia albida* (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 582 (1923). Holotype. Colombia, *Lindig 748* (H-NYL 22766!).

Thallus light yellow-grey, verrucose, with loose cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia immersed-erumpent, angular-rounded, 0.5–1 mm diam.; disc exposed, grey-brown, white-pruinose; margin lobulate, white, partly with split between excipulum and thalline margin. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 60–70 µm

high, clear; paraphyses unbranched. Ascospores 8/ascus, 7–15-septate, 20–35 × 6–8 µm, oblong, with slightly thickened septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Chapsa albida* is a resurrected species in the *C. alborosella* complex. The species in this complex all have small, transversely septate ascospores but differ in thallus morphology, development of a cortex, ascospore amyloidity, and secondary chemistry. *Chapsa albida* is most similar to *C. alborosella* but has a more yellowish, verrucose, loosely corticate thallus and larger ascospores. It was previously considered a synomym of *C. cinchonarum* (Fée) Frisch, but that species has an ecorticate thallus and the apothecia are often irregularly elongate (Frisch 2006). Also similar is *C. chionostoma* (see below), which differs in the smaller ascospores with less septa and the dense thallus cortex. *Chapsa albida* appears to be a montane rain forest species.

Specimens examined:—COSTA RICA. Cartago: Tapantí National Park; 83° 47' W, 09° 44' N, 1300–1400 m; Apr 2003, *Chaves 511* (INB). Puntarenas: Las Tablas Protection Zone, Los Portones Section (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km ENE of San Vito, 5 km on gravel road from Progreso to Las Tablas, roadside; 82° 48' W, 8° 55' N, 1600 m; montane rain forest zone, abandoned roadside pasture with dense shrubs and treelets, on bark (lower stem), semi-exposed; Jun 2002, *Sipman 47931* (B).

***Chapsa alborosella* (Nyl.) Frisch** (Fig. 6G)

Chapsa alborosella (Nyl.) Frisch, Biblioth. Lichenol. 92: 91 (2006); *Graphis alborosella* Nyl., Ann. Sci. Nat. Bot. Sér. 4, 19: 372 (1863); *Ocellularia alborosella* (Nyl.) R. Sant., Symb. Bot. Upsal. 12(1): 308 (1952); *Chroodiscus alborosellus* (Nyl.) Kalb, Lich. Neotrop. Fasc. XX: 8 (1991). Holotype. Colombia, *Lindig 2694* (H-NYL 7635!).

Thallus light grey-green, smooth to uneven, ecorticate; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.3–1.2 mm diam.; disc exposed, flesh-colored to pale brown, white-pruinose; margin lobulate, fused, pale brown, felty white-pruinose. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present, distinct. Hymenium 40–60 µm high, clear; paraphyses unbranched, thick, apically moniliform. Ascospores 8/ascus, 5–9-septate, 15–25 × 4–5 µm, fusiform, with slightly thickened septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Chapsa alborosella* is a commonly collected species which was reported before from Costa Rica by Breuss (2000); it is found in lowland to montane rain forest in semi-exposed situations. It can be recognized by the pale greenish thallus, which is ecorticate but compact and not farinose, and by the felty white-pruinose apothecial margins. *Chapsa platycarpella* (see below) had been considered a synonym of this species by Hale (1978) and Matsumoto (2000), but differs clearly in its endoperidermal, corticate thallus and non-felty apothecial margins, as well as the smaller ascospores with less septa.

Specimens examined:—COSTA RICA. Alajuela: Refugio Nacional de Vida Silvestre Mixto Maquenque; 84° 11' W, 10° 42' N, 0–100 m; Apr 2005, *Chaves 2306* (INB). Los Chiles, plantación de *Melina*; 84° 41' W, 11° 01' N, 0–100 m; Feb 2009, *Chaves 3662* (INB). San Ramón Forest Reserve, near house at Río Lorencito, 5 km NE of Cerro Jabonal; 84° 37' W, 10° 13' N, 1000 m; humid, mossy forest with many ferns on mountain ridge, on thin trunk in undergrowth; Nov 1988, *Sipman et al. 41958* (B, CR), *41962* (B, CR). Volcán Tenorio National Park, Pilón section; 84° 59' W, 10° 42' N, 700–800 m; secondary forest; Jul 2004, *López 5608* (INB). Cartago: On road Limón-Turrialba, about halfway between Siquirres and Chitaría; 83° 30' W, 10° 03' N, 700 m; on trunks in grazed parkland with groves; Jan 1979, *Sipman 12309* (U), *12310* (B), *12339* (U). CATIE Agricultural Research Centre near Turrialba; 83° 40' W, 9° 55' N, 600 m; epiphytic in undergrowth of primary forest on steep slope along river, Los Espaveles trail; Nov 1988, *Sipman & Döbbeler 42376* (B, CR). Limón: Hitoy Cerere Biological Reserve; 83° 01' W, 9° 40' N, 200–300 m; slightly disturbed primary forest; Mar 2004, *Will-Wolf 12711* (INB, WIS). Puntarenas: La Amistad International Park, Altamira Station (La

Amistad Pacífico Conservation Area), Talamanca Ridge, 20 km N of San Vito near Finca Colorado, trail to Casa Coca; 82° 59' W, 9° 02' N, 1800 m; montane rain forest zone, abandoned pasture with forest remnants, on bark (lower stem), partially shaded; July 2002, *Sipman 48063f* (B, INB). Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), partially shaded; Feb 1997, *Lücking 97-245* (CR, F, INB). San Vito de Coto Brus, Las Cruces Biological Station; 82° 58' W, 8° 47' N, 1200 m; on ridge beyond Río Java, on trunks and undergrowth of disturbed primary forest; Oct 2004, *Sipman 53249* (B, INB).

***Chapsa astroidea* (Berk. & Broome) Cáceres & Lücking** (Fig. 6H)

Chapsa astroidea (Berk. & Broome) Cáceres & Lücking, Libri Bot. 22: 51 (2007); *Platygrapha astroidea* Berk. & Broome, J. Linn. Soc., Bot., 14: 109 (1875); *Cryptodiscus astroideus* (Berk. & Broome) Sacc., Syll. Fung. 8: 674 (1889); *Ocellularia astroidea* (Berk. & Broome) Hale, Mycotaxon 7: 377 (1978); *Thelotrema astroideum* (Berk. & Broome) Hale, Mycotaxon 11: 131 (1980). Lectotype (Hale 1980: 253). Sri Lanka, *Thwaites 629* (K!).

Thallus yellow-olive, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.5–2.5 mm diam.; disc exposed, flesh-colored to pale brown, thinly white-pruinose; margin lobulate to recurved, fused, pale brown, thinly white-pruinose. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 40–60 µm high, clear; paraphyses unbranched, thick, apically capitate. Ascospores 8/ascus, 3–7-septate, 12–20 × 4–5 µm, oblong with distal ends tapering, with slightly thickened septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Chapsa astroidea* is a very conspicuous species due to its corticate thallus and large, contrasting, distinctly chroodiscoid apothecia. Although similar to *C. alborosella* (see above) in ascospore type, it differs by the corticate thallus and instead resembles the species in the *C. sublilacina* complex, which have much larger ascospores with more numerous septa. *Chapsa astroidea* also reminds of *Acanthotrema brasilianum* (see above), which can be distinguished by the apically spinulose paraphyses and the partly splitting cortex. Mangold *et al.* (2009) synonymized *C. platycarpella* (see below) with *C. astroidea*; both agree in ascospore type and the dense cortex, but *C. platycarpella* has a thinner, endoperidermal thallus and distinctly blue-grey-pruinose apothecial discs, as well as slightly smaller ascospores, and is here kept separate. Cáceres (2007) separated both species on account of the thickness of the ascospore septa, but this difference could not be confirmed based on the available material, including types. A similar species from Australia, *C. halei* Mangold, differs in its white-grey, ecorticate thallus, fissurinoid apothecia, and smaller ascospores. *Chapsa astroidea* prefers shaded tree trunks in lowland to montane rain forest.

Specimens examined:—COSTA RICA. Alajuela: Volcán Tenorio National Park, Pilón Biological Station (Arenal-Tempisque Conservation Area), Tilarán Ridge, 140 km NW of San José, 25 km NNW of Tilarán, near Bijagua, main trail through forest to crater; 84° 59' W, 10° 43' N, 700–900 m; lower montane cloud forest zone, partly disturbed primary forest, on bark (lower trunk), semi-exposed; Mar 2004, *Lücking 17267d* (CR, F, INB, USJ). Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, round trail NW of station (Sendero Sirena and Sendero Guanacaste); 83° 35' W, 8° 29' N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (lower stem), partially shaded; Apr 2003, *Lücking 16240* (F); ibid., trail to beach S of station (Sendero Los Naranjos); 83° 35' W, 8° 29' N, sea level; lowland coastal rain forest zone, coastal secondary forest and closed secondary vegetation on sandy soil, on bark (lower trunk), partially shaded; Apr 2003, *Buck 44132* (CR, NY), *Lücking 16382a* (F, INB); ibid., on bark (lower stem), partially shaded; Apr 2003, *Lücking 16392e* (CR, F, ,

INB, USJ). Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), partially shaded; Feb 1997, *Lücking 97-246* (F, CR, INB).

***Chapsa chionostoma* (Nyl.) Rivas Plata & Mangold** (Fig. 7A)

Chapsa chionostoma (Nyl.) Rivas Plata & Mangold in Rivas Plata *et al.*, Lichenologist 42: 182 (2010); *Thelotrema chionostomum* Nyl., Ann. Sci. Nat., Bot., Ser. 4, 19: 329 (1863); *Ocellularia chionostoma* (Nyl.) Riddle, Bull. Torrey Bot. Club 44: 325 (1917). Lectotype (Hale 1978: 16): Cuba, *Wright 3* (FH!).
Ocellularia phlyctellacea Müll. Arg., Bull. Soc. Bot. Belgique 32: 146 (1893). Lectotype (Hale 1978: 16): Costa Rica, *Pittier 6106* (G!).

Thallus white-grey, smooth to uneven, with prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.2–0.3 mm diam.; disc exposed, pale brown, white-pruinose; margin lobulate but lobes crumbling, fused, pale brown, white-pruinose. Columella absent. Excipulum paraplectenchymatous, brown; periphysoids indistinct. Hymenium 40–60 µm high, clear; paraphyses unbranched, thick, apically moniliform. Ascospores 8/ascus, 3–5-septate, 10–18 × 4–6 µm, fusiform, with slightly thickened septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Chapsa chionostoma* is an inconspicuous species that is easily confused with *C. albida*, *C. alborosella*, *C. astroidea* and similar species (see above). It differs mainly in its small apothecia with indistinctly lobulate, crumbling margin and ascospores, in combination with the corticate thallus giving it a *Phlyctis*-like appearance.

Chapsa defecta* Lücking, *spec. nov. (Fig. 7B)
MycoBank #800071

Differing from *Chapsa sublilacina* in the absence of secondary substances.

Holotype:—COSTA RICA. Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, round trail NW of station (Sendero Sirena and Sendero Guanacaste); 83° 35' W, 8° 29' N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (lower trunk), partially shaded; Apr 2003, *Lücking 16244* (CR; isotypes: F, INB-0004003207, USJ).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 1–3 mm diam.; disc exposed, flesh-colored; margin lobulate to recurved, fused but sometimes lamellate, flesh-colored. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 120–150 µm high, clear; paraphyses unbranched. Ascospores 2–4/ascus, 11–15-septate, 80–110 × 10–14 µm, cylindrical, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This new species is part of a complex of species centered around *Chapsa sublilacina* (see below), all having similar thallus morphology and ascospore type. Four taxa are here distinguished: with or without stictic acid and satellite substances, and with either large, compact, finely granular soralia or small, irregular, coarse soralia. The form with large soralia, *C. thallotrema* (see below), always contains stictic acid, whereas the form with small soralia, described below as *C. defectosorediata*, does not produce secondary substances. The problem arises with the non-sorediate forms, which only differ chemically and might represent either sister species of the sorediate forms or be conspecific with either of them, depending on their

chemistry. Phylogenetic studies suggest that sorediate and non-sorediate counterparts are either part of a single species (Myllys *et al.* 1999; Molina *et al.* 2002; Cubero *et al.* 2004; Lohtander *et al.*, 2008; Lücking *et al.* 2008b; Prashanth *et al.* 2008) or more rarely form two or several distinct species (Grube & Kroken 2000; Kroken & Taylor 2001; Lohtander *et al.* 2009; Tehler *et al.* 2010; Miadlikowska *et al.* 2011). Since we do not yet have molecular data to test these hypotheses in the present case, we have opted to keep the non-sorediate and sorediate forms separate at this time, pending further study. This is supprted by geographic differentiation observed in *C. thallotrema*: in Costa Rica, the species is quite abundant but without exception only found with soralia; similarly abundant are the apotheciate forms assigned to *C. sublilacina*. In Panama, we found the two forms also frequently side by side, but with *C. thallotrema* also producing apothecia.

Chapsa defectosorediata* Lücking, *spec. nov. (Fig. 7C)
MycoBank #800072

Differing from *Chapsa thallotrema* in the smaller, dispersed soralia and the absence of secondary substances.

Chapsa sorediata Lücking in Rivas Plata *et al.*, Lichenologist 42: 153 (2010) [nom. inval., non *Chapsa sorediata* Kalb]. Original material: not indicated.

Holotype:—COSTA RICA. Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, round trail NW of station (Sendero Sirena and Sendero Guanacaste); 83° 35' W, 8° 29' N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (lower stem), partially shaded; Apr 2003, *Lücking 16210* (CR; isotypes: F, INB-0004002821, USJ).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex, sorediate; soralia scattered, irregular to capitate, 0.2–0.4 mm diam.; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 1–3 mm diam.; disc partially covered to exposed, flesh-colored; margin lobulate to recurved, often layered, flesh-colored to beige. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 120–180 µm high, clear; paraphyses unbranched. Ascospores 2–8/ascus, 13–17-septate, 70–90 × 10–15 µm, cylindrical, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This new species belongs in the *Chapsa sublilacina* aggregate and is distinguished from the *C. sublilacina* by the scattered, small soralia and the absence of secondary substances. It is the sorediate counterpart of *C. defecta* (see above) and both may represent the same taxon; however, we have kept the sorediate and non-sorediate form separate until molecular data are available to confirm either hypothesis. The species was originally intended to be named *C. sorediata* Lücking and under that name included in a key (Rivas Plata *et al.* 2010); however, at the time the key had been submitted for publication, another species was published under the same name, *C. sorediata* Kalb (2009), which requires to publish the present species validly with a different name. *Chapsa sorediata* Kalb is very different from *C. defectosorediata* both in thallus morphology, ascospore size, and chemistry, and not closely related to that species.

***Chapsa dilatata* (Müll. Arg.) Kalb** (Fig. 7D)

Chapsa dilatata (Müll. Arg.) Kalb, Biblioth. Lichenol. 99: 140 (2009); *Ocellularia dilatata* Müll. Arg., J. Linn. Soc. London, Bot. 30: 452 (1895); *Thelotrema dilatatum* (Müll. Arg.) Hale, Mycotaxon 11: 131 (1980). Holotype. Brazil, *Glaziou 6631* p.p. (G!).

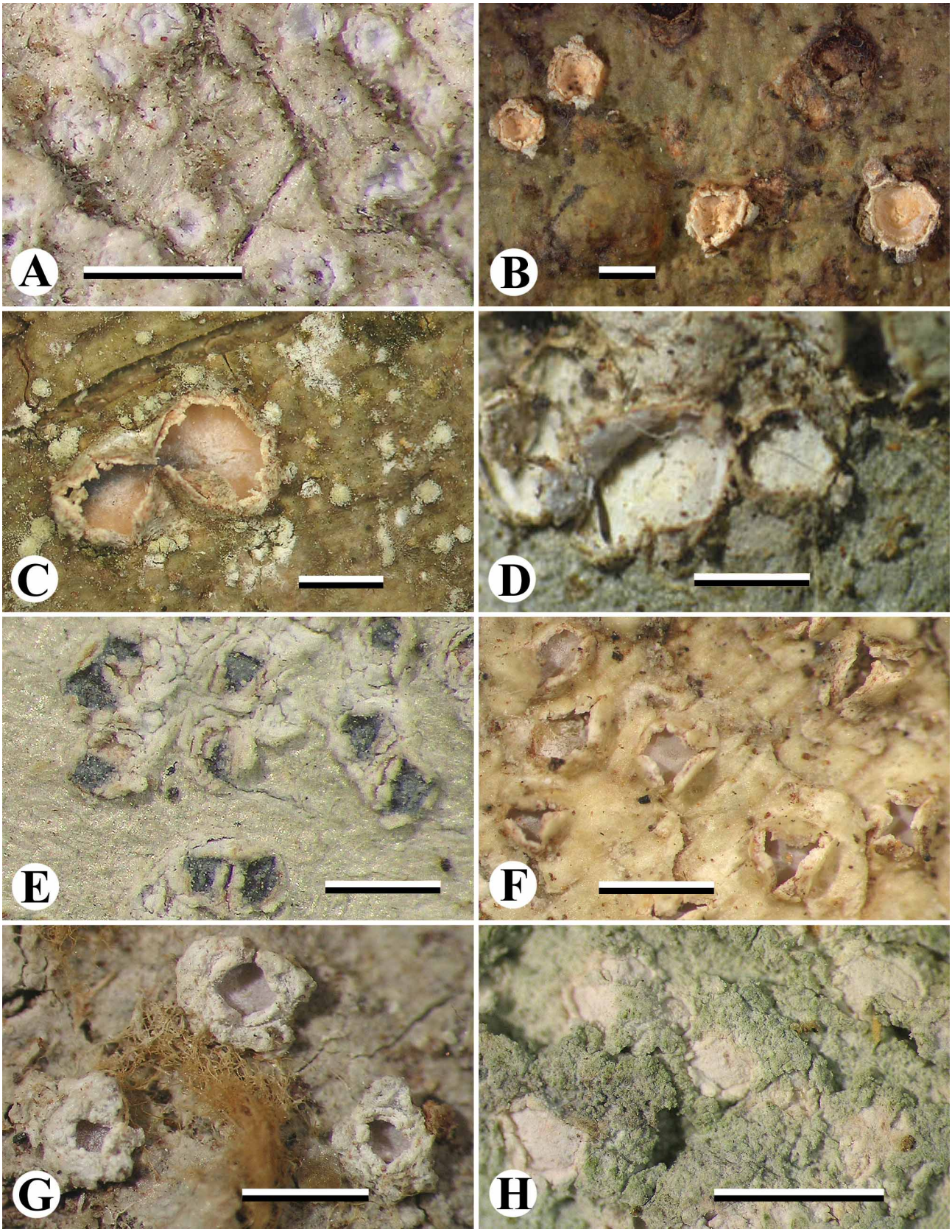

FIGURE 7. A. *Chapsa chionostoma*. B. *Chapsa defecta*. C. *Chapsa defectosorediata*. D. *Chapsa dilatata*. E. *Chapsa discoides*. F. *Chapsa dissuta*. G. *Chapsa esslingeri*. H. *Chapsa farinosa*. Scale = 1 mm.

Thallus white-grey, smooth to uneven, ecorticate; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular to elongate, 0.7–2 × 0.5–1 mm; disc exposed, grey-brown, thickly white-pruinose; margin lobulate to recurved, fused, grey-brown, white-pruinose. Columella absent. Excipulum paraplectenchymatous, pale brown; periphysoids present. Hymenium 60–70 µm high, clear; paraphyses unbranched, apically moniliform. Ascospores 8/ascus, 5–9-septate, 15–30 × 5–8 µm, oblong, with thickened septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: stictic, constictic, hypoconstictic and cryptostictic acids.

Remarks:—*Chapsa dilatata* somewhat resembles *C. alborosella* and relatives, but is well-characterized by the often elongate apothecia with thick white pruina and the stictic acid chemosyndrome. The species is rather common in parts of South America but appears to be rare in Central America. Revision of material from South America and Sri Lanka (Hale 1981) suggests that two separate species are hidden under this name, one with greenish thallus and more or less rounded apothecia with recurved lobules and one with white-grey thallus and often elongate apothecia with irregular, erect lobules and thick white pruina on the apothecial disc (Cáceres 2007). The Costa Rican material belongs to the latter which also agrees well with the type.

Specimens examined:—COSTA RICA. Puntarenas: Cordillera de Tilarán, Monteverde, near the cheese factory; 84° 49' W, 10° 18' N, 1450 m; premontane rain forest zone, forest relics among pasturefields, on trunks; Jan 1979, *Sipman 12085* (U).

Chapsa discoides* (Stirt.) Lücking, *comb. nov. (Fig. 7E)
MycoBank #800046

Graphis discoides Stirt., *Proc. Roy. Phil. Soc. Glasgow* 13: 187 (1881). Lectotype (Patwardhan & Kulkarni, annot. 1976): India, Watt s.n. (BM!).
Chapsa velata (Müll. Arg.) Cáceres & Lücking, Libri Bot. 22: 54 (2007); *Thelotrema velatum* Müll. Arg., Bull. Soc. Bot. Belgique 32: 147 (1893). Holotype. Costa Rica, *Pittier 6123* (G!).
Thelotrema deightonii C. W. Dodge, Beih. Nova Hedwigia 12: 100 (1964). Holotype. Sierra Leone, *Deighton M5856* (BM!; isotype: FH!).

Thallus light grey, smooth to uneven, ecorticate; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.3–0.5 mm diam.; disc exposed, brown, thickly white-pruinose and therefore appearing blue-grey; margin lobulate to recurved, pale brown, white-pruinose. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 80–100 µm high, clear; paraphyses unbranched, thick, apically moniliform. Ascospores 2–4(–8)/ascus, muriform, 30–60 × 12–20 µm, ellipsoid, with thin septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This species is very similar to *Chapsa pseudophlyctis* (Nyl.) Frisch, but differs in the white-grey thallus and blue-grey apothecial discs. In *C. pseudophlyctis*, the thallus is olive and the apothecial disc is pale brown with a thin white pruina. *Chapsa leprocarpoides* (Hale) Cáceres & Lücking has a free excipulum, smaller ascospores, and often aggregate apothecia. *Chapsa leprocarpa* (see above) and relatives differ in single-spored asci with larger ascospores. *Chapsa discoides* is one of few species treated here that appears to be restricted to the drier northeastern parts of Costa Rica, being dominated by evergreen moist and semideciduous dry forest with marked dry season. Stirton's name was previously overlooked as it had been described in *Graphis*, but turned out to be an earlier epithet for the species thus far treated as *C. velata* (Rivas Plata *et al.* 2010a).

Specimens examined:—COSTA RICA. Lomas de Barbudal Biological Reserve, Lomas de Barbudal Station (Tempisque Conservation Area), Río Tempisque Bassin, 140 km WNW of San José and 20 km WSW of Bagaces, trail from station to Río Barbudal; 85° 22' W, 10° 30' N, 100 m; lowland to lower montane moist forest zone, disturbed gallery forest and forest remnants, on bark (twig, fallen), Mar 2003, *Trest 1343b* (INB); ibid., on bark (lower trunk), semi-exposed; Mar 2003, *Lücking 16100b* (F); ibid., on bark (lower stem),

exposed; Mar 2003, *Lücking 16108b* (F). Monte Alto Forest Reserve, Monte Alto Biological Station (Tempisque Conservation Area), Nicoya Pensinsula, 150 km W of San José, 10 km SSE of Nicoya, near Hojancha, surroundings of station; 85° 24' W, 10° 02' N, 450–550 m; lowland to lower montane moist forest zone, planted, shaded trees near station facilities, on bark (lower stem), semi-exposed; Mar 2004, *Lücking 17650a* (CR, F, INB, USJ).

***Chapsa dissuta* (Hale) Mangold** (Fig. 7F)

Chapsa dissuta (Hale) Mangold in Mangold *et al.*, Fl. Austral. 57: 653 (2009); *Ocellularia dissuta* Hale, Smithson. Contr. Bot. 38: 20 (1978); *Thelotrema dissutum* (Hale) Hale, Mycotaxon 11: 131 (1980). Holotype. Panama, *Hale 43520* (US!).

Thallus light grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.5–0.8 mm diam.; disc partially covered, pale brown, thinly white-pruinose; margin fissured-lobulate, fused or proper excipulum partly free, pale brown. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids apparently absent. Hymenium 50–60 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3-septate, 10–12 × 4–6 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, weakly I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Chapsa dissuta* is a rather unusual species in the genus in having almost fissurine, yet rounded, apothecia and a dense, prosoplectenchymatous cortex. In many aspects it resembles a *Fissurina*, and since the clade containing *Fissurina* is known to also include thelotremoid taxa (Rivas Plata *et al.* 2012a), it cannot be ruled out that *Chapsa dissuta* is in fact a *Fissurina* or at least related to that genus. A very similar taxon is *C. lassae* (see below), which chiefly differs in having distinct periphysoids and non-amyloid ascospores with thin septa. Another related species appears to be *C. perdissuta*, newly described below, which, however, has large, muriform ascospores.

Specimens examined:—COSTA RICA. Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, second part of trail from Los Patos to Sirena station; 83° 33' W, 8° 32' N, sea level; lowland rain forest zone, oldgrowth secondary forest and closed secondary vegetation, on bark (lower stem), semi-exposed; Apr 2003, *Sipman 51103a* (B, INB).

Chapsa esslingeri* (Hale) Sipman, *comb. nov. (Fig. 7G)
MycoBank #800059

Ocellularia esslingeri Hale, Smithson. Contr. Bot. 38: 20 (1978); *Thelotrema esslingeri* (Hale) Hale, Mycotaxon 11: 131 (1980). Holotype. Panama, *Esslinger 4626* (US!).

Thallus light grey-green, smooth to uneven, with loose cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent to prominent, angular-rounded, 0.7–1.1 mm diam.; disc partially covered, flesh-colored to pale brown, thinly white-pruinose; margin lobulate, fused, pale brown, white-pruinose. Columella absent. Excipulum paraplectenchymatous, pale brown; periphysoids present. Hymenium 70–90 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–7-septate, 15–23 × 5–7 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: stictic and constictic acids.

Remarks:—This species in many aspects resembles *Chapsa dilatata* (ascospores, chemistry), but differs morphologically in the always rounded (never elongate), usually prominent apothecia with thin pruina and the

more compact, distinctly greenish thallus. Hale (1978) reported an unidentified P– compound from the type, but TLC revealed presence of the stictic acid chemosyndrome. *Chapsa phlyctidioides* agrees with *C. esslingeri* in general habit and ascospore size and septation, but lacks a thallus cortex, the apothecia are smaller, and the ascospores are non-amyloid.

Specimens examined:—Not yet found in Costa Rica but reported from Panama (Hale 1978).

Chapsa farinosa* Lücking & Sipman, *spec. nov. (Fig. 7H)
MycoBank #800073

Differing from *Chapsa alborosella* in the ecorticate, strongly farinose thallus.

Holotype:—COSTA RICA. Limón: Gandoca-Manzanillo Wildlife Refuge, Manzanillo Section (La Amistad Caribe Conservation Area), Manzanillo, 170 km ESE of San José, 65 km SE of Limón, trail along beach; 82° 53' W, 9° 38' N, sea level; lowland coastal moist forest zone, disturbed coastal vegetation with *Cocos nucifera*, *Coccoloba uvifera*, and *Rhizophora mangle*, on bark (lower trunk), partially shaded; Mar 2004, *Lücking 17088c* (CR; isotype: F).

Thallus white-grey, distinctly farinose, ecorticate; photobiont layer and/or medulla with abundant clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.3–0.5 mm diam.; disc exposed, flesh-colored to pale brown, white-pruinose; margin lobulate to recurved, fused, pale brown, felty white-pruinose. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 50–70 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 7–9-septate, 20–30 × 4–6 µm, oblong, with slightly thickened septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This is a new species in the difficult *Chapsa alborosella* aggregate. It differs from the latter chiefly in the whitish, farinose thallus lacking any traces of a cortex. *Chapsa albida* (see above) is most similar but has a compact, coarsely verrucose thallus with loose cortex. *Chapsa dilatata* (see above) also differs in the compact thallus, the larger, often elongate apothecia with thick white pruina, and the presence of the stictic acid chemosyndrome. Another species, *C. cinchonarum* (Fée) Frisch, which has not yet been found in Costa Rica, can be easily confused with *C. farinosa* but has a compact thallus with loose cortex and often elongate apothecia. The new species appears to be a coastal rain forest taxon.

Additional specimens examined (paratypes):—COSTA RICA. Alajuela: Volcán Tenorio National Park, Pilón Biological Station (Arenal-Tempisque Conservation Area), Tilarán Ridge, 140 km NW of San José, 25 km NNW of Tilarán, near Bijagua, access road to station and river; 84° 59' W, 10° 43' N, 700 m; lower montane cloud forest zone, exposed trees and fence posts along pasture, on bark (lower trunk) of *Syzygium jambos*, exposed; Mar 2004, *Aptroot 60580* (BR, INB). Limón: Gandoca-Manzanillo Wildlife Refuge, Manzanillo Section (La Amistad Caribe Conservation Area), Manzanillo, 170 km ESE of San José, 65 km SE of Limón, trail along beach; 82° 53' W, 9° 38' N, sea level; lowland coastal moist forest zone, disturbed coastal vegetation with *Cocos nucifera*, *Coccoloba uvifera*, and *Rhizophora mangle*, on bark (lower trunk), partially shaded; Mar 2004, *Lücking 17088k* (F, INB). Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, trail to beach S of station (Sendero Los Naranjos); 83° 35' W, 8° 29' N, sea level; lowland coastal rain forest zone, coastal secondary forest and closed secondary vegetation on sandy soil, on bark (lower trunk), semi-exposed; Apr 2003, *Lücking 16380b* (F).

Chapsa hiata* (Hale) Sipman, *comb. nov. (Fig. 8A)
MycoBank #800065

Thelotrema hiatum Hale, Smithson. Contr. Bot. 38: 44 (1978). Holotype. Panama, *Hale 43485* (US!).

Thallus white-grey, smooth to uneven, ecorticate; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.4–0.7 mm diam.; disc partially covered, grey-black, white-pruinose; margin lobulate, fused, white-grey. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 80–100 µm; paraphyses unbranched, thick. Ascospores 8/ascus, submuriform with 3 transverse septa and 0–1 longitudinal septa per segment, 12–15 × 6–7 µm, ellipsoid, with slightly thickened septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This rare species closely resembles *Chapsa alborosella* and relatives but is set apart by the submuriform ascospores.

Specimens examined:—COSTA RICA. Guanacaste: Along Río Liberia northeast of Liberia; 100 m; Jan 1930, *Dodge et al. s.n.* (FH; as *Phaeotrema jamaicense* Müll. Arg.).

***Chapsa laceratula* (Müll. Arg.) Rivas Plata & Lücking** (Fig. 8B)

Chapsa laceratula (Müll. Arg.) Rivas Plata & Lücking in Rivas Plata *et al.*, Lichenologist 42: 183 (2010). *Thelotrema laceratulum* Müll. Arg., Flora 70: 399 (1887); *Topeliopsis laceratula* (Müll. Arg.) Mangold in Mangold *et al.*, Fl. Australia 57: 659 (2009). Lectotype (Mangold *et al.* 2009: 659): Australia, *Sayer s.n.* (G!).

Thallus light grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.3–0.8 mm diam.; disc covered, flesh-colored to pale brown, thinly white pruinose; margin fissured to lobulate, layered, pale brown, white-pruinose. Columella absent. Excipulum paraplectenchymatous, pale yellow; periphysoids present. Hymenium 150–220 µm high, clear; paraphyses unbranched. Ascospores 1–2/ascus, richly muriform, 70–170 × 20–35 µm, ellipsoid, with slightly thickened septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Chapsa laceratula* belongs in a group of species with layered excipulum which covers the disc, resembling the apothecia of *Topeliopsis*, and was combined in the latter genus by Mangold *et al.* (2009). However, corticolous species with *Topeliopsis*-like apothecia and a well-developed thallus with prosoplectenchymatous cortex have all been included in *Chapsa* (Rivas Plata *et al.* 2010a), and the position of *C. laceratula* was confirmed using molecular methods (Rivas Plata *et al.* 2012c).

Specimens examined:—COSTA RICA. Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, second part of trail from Los Patos to Sirena station; 83° 33' W, 8° 32' N, sea level; lowland rain forest zone, oldgrowth secondary forest and closed secondary vegetation, on bark (lower trunk), partially shaded; Apr 2003, *Lücking 16365a* (F, INB).

***Chapsa lassae* Mangold** (Fig. 8C)

Chapsa lassae Mangold in Mangold *et al.*, Fl. Australia 57: 653 (2009). Holotype. Australia, *Mangold 35zq* (CANB!; isotypes: BRI!, F!).

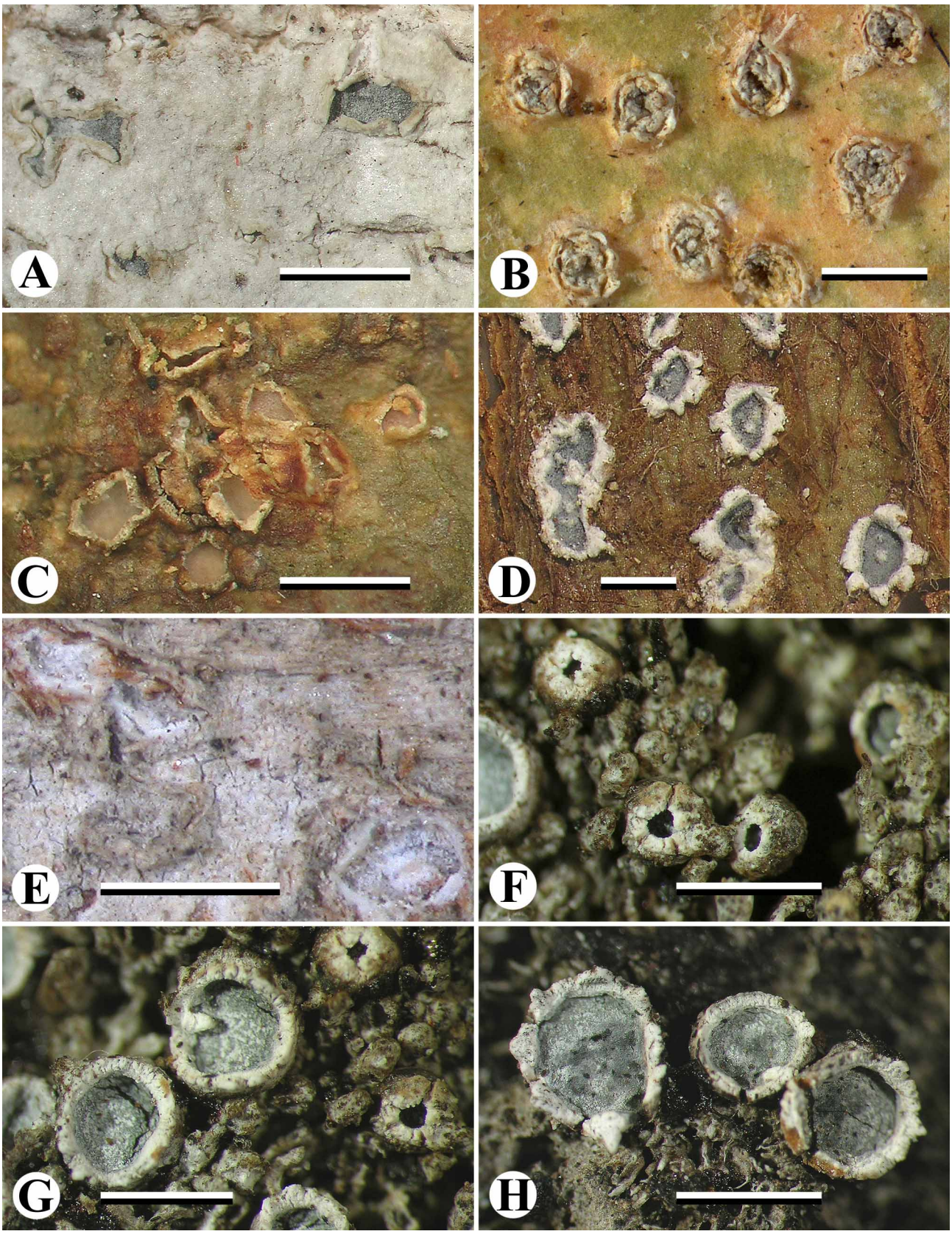

FIGURE 8. A. *Chapsa hiata*. B. *Chapsa laceratula*. C. *Chapsa lassae*. D. *Chapsa leprieurii*. E. *Chapsa leprocarpa*. F–H. *Chapsa meridensis*. Scale = 1 mm.

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.3–0.6 mm diam.; disc exposed to partly covered, pale grey-brown, thinly white-pruinose; margin lobulate to recurved, fused, pale brown, white-pruinose. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 50–60 µm high, clear; paraphyses unbranched, thick, apically capitate. Ascospores 8/ascus, 10–15 × 4–6 µm, ellipsoid, with thin septa and rectangular lumina, I– (non-amyloid), 3–5-septate. Secondary chemistry: no substances detected by TLC.

Remarks:—This species is remarkably similar to *Chapsa dissuta* (see above) and the major difference lies in the ascospores, which in the latter have thickened septa and are distinctly amyloid. A probably related species is *Chroodiscus exfoliatus* Kalb (Kalb 2001), which agrees in external morphology and ascospore size and septation. The ascospores are described as with thickened septa but I– (non-amyloid) and hence intermediate between *C. dissuta* and *C. lassae*; however, what sets *Chroodiscus exfoliatus* apart are the apically spinulose paraphyses, a character only found in *Acanthotrema*. The latter genus has thin-walled ascospores. Obviously this complex requires further study, especially as these species somewhat resemble the genus *Fissurina* and several species in that genus have apically spinulose paraphyses as well.

Specimens examined:—COSTA RICA. Heredia: La Selva Protection Zone, La Selva Biological Station (Cordillera Volcánica Central Conservation Area), Volcánica Central Ridge, 55 km N of San Jose; 84° 03' W, 10° 26' N, 50 m; lowland rain forest zone, disturbed primary and secondary forest bordering experimental tree plantations, on bark (lower trunk), partially shaded; 2006, *Lizano et al. PR-9-9* (USJ).

***Chapsa leprieurii* (Mont.) Frisch** (Fig. 8D)

Chapsa leprieurii (Mont.) Frisch, Biblioth. Lichenol. 92: 105 (2006); *Stictis leprieurii* Mont., Ann. Sci. Nat., Bot., Sér. 4, 3: 97 (1855); *Phaeotrema leprieurii* (Mont.) Sherwood, Mycotaxon 5: 203 (1977); *Thelotrema leprieurii* (Mont.) Hale, Mycotaxon 11: 131 (1980). Lectotype (Hale 1981: 258). French Guiana, *Leprieur 804* (PC; isolectotype: G!).

Thelotrema leucastrum Tuck., Proc. Amer. Acad. Arts Sci. 6: 269 (1864); *Phaeotrema leucastrum* (Tuck.) Zahlbr., Cat. Lich. Univ. 2: 608 (1923). Lectotype (Frisch 2006: 105). Cuba, *Wright s.n.* (FH-TUCK!; isolectotype: H-NYL 22662!; Wright, Lich. Cub. 158).

Thelotrema leucastrum var. *difforme* Tuck., Proc. Amer. Acad. Arts Sci. 6: 269 (1864); *Thelotrema difforme* (Tuck.) Vain., Ann. Acad. Sci. Fenn., Ser. A, 15(6): 194 (1921); *Phaeotrema leucastrum* var. *difforme* (Tuck.) Zahlbr., Cat. Lich. Univ. 2: 608 (1923). Holotype. Cuba, *Wright s.n.* (FH-TUCK!; isotype: H-NYL 22664!; Wright, Lich. Cub. 159).

Graphis subnivescens Nyl., Bol. Soc. Brot. 4: 211 (1886); *Phaeotrema subnivescens* (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 387 (1923). Holotype. São Tomé, *Moller s.n.* (H-NYL 7507!).

Graphis phlyctidea Vain., Ann. Acad. Sci. Fenn., Ser. A, 15(6): 137 (1921); *Phaeographis phlyctidea* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 383 (1923). Holotype. Philippines, *Elmer 14646* (TUR-VAIN 27523!; isotype: FH!).

Thelotrema confluens Vain., Ann. Acad. Sci. Fenn., Ser. A, 15(6): 193 (1921); nom. illeg., non *Thelotrema confluens* Kremp.; *Ocellularia confluentula* Zahlbr., Cat. Lich. Univ. 2: 587 (1923); nom. nov. Holotype. Philippines, *Elmer 14641* (TUR-VAIN 26908!).

Thallus brown, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer with scattered clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 1–2 mm diam.; disc exposed, pale brown, white-pruinose; margin lobulate to recurved, fused, pale brown, felty white-pruinose. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 50–70 µm high, clear; paraphyses unbranched, thick, apically moniliform. Ascospores 8/ascus, 3-septate, 12–16 × 5–6 µm, ellipsoid, with thick septa and lens-shaped lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Chapsa leprieurii* is a very characteristic taxon, due to the strongly contrasting brown (often orange- or red-brown), corticate thallus and large apothecia with pruinose disc and thick, felty margin, and the small, brown ascospores. It cannot be confused with any other species in the family. The taxon appears to prefer lowland rain forest.

Specimens examined:—COSTA RICA. Heredia: La Selva Protection Zone, La Selva Biological Station (Cordillera Volcánica Central Conservation Area), Volcánica Central Ridge, 55 km N of San Jose, Arboleda; 84° 03' W, 10° 26' N, 50 m; lowland rain forest zone, disturbed primary and secondary forest, on bark (lower trunk), partially shaded; Feb 1992, Lücking 1316 (F); ibid., Feb 1997, *Lücking 97-239* (F); ibid., Oct 2002, *Lücking 16047* (F). Puntarenas: Cocos Island National Park, Río Genio; 87° 03' W, 05° 32' N, 0–100 m; Jun 2005, *Fletes 7754* (INB).

***Chapsa leprocarpa* (Nyl.) Frisch** (Fig. 8E)

Chapsa leprocarpa (Nyl.) Frisch, Biblioth. Lichenol. 92: 108 (2006); *Graphis leprocarpa* Nyl., Acta Soc. Sci. Fenn. 7: 472 (1863); *Thelotrema leprocarpum* (Nyl.) Tuck., Gen. Lich.: 139 (1872). Holotype. U.S.A., *Hale 111* (FH!; isotype: H-NYL 6839!).

Thelotrema colobicum Nyl., Bull. Soc. Linn. Normandie, Sér. 2, 7: 169 (1873). Holotype. India (Andaman Islands), *Kurz 43* (M!; isotype: H-NYL 22493!).

Thelotrema poeltii Patw. & C. R. Kulk, Norw. J. Bot. 24: 130 (1977). Holotype. India, *Prabhu & Nagarkar 74.2195* (AMH, not seen).

Thallus light grey-olive, smooth to uneven, ecorticate; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.5–0.7 mm diam.; disc exposed, pale brown, white-pruinose with scattered, shiny cystals; margin lobulate, pale brown, felty white-pruinose. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 80–100 µm high, clear; paraphyses unbranched, thick, apically moniliform. Ascospores single, muriform, 60–110 × 20–40 µm, ellipsoid, with slightly thickened septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Chapsa leprocarpa* forms part of a difficult species complex comprising taxa with single, large, muriform ascospores. As in the *C. alborosella* aggregate, the species differ in thallus and apothecial morphology, ascospore amyloidity, and chemistry. Most similar are *Chapsa patens* (Nyl.) Frisch, with larger ascospores and recurved margin, and *C. grossomarginata* (T. Matsumoto) Mangold, with 2-spored asci (Rivas Plata *et al.* 2010a). *Chapsa leprocarpa* is predominantly found in semi-exposed situations in (lower) montane rain forest.

Specimens examined:—COSTA RICA. Guanacaste: Volcán Tenorio National Park, Alto Masis Section (Arenal-Tilarán Conservation Area), Tilarán Ridge, 125 km NW of San José, 15 km NNW of Tilarán, near Tierras Morenas, access road to station; 85° 00' W, 10° 36' N, 850–900 m; lower montane moist forest zone, exposed trees and fence posts and forest regrowth along savanna-like pasture, on bark (lower trunk), fully exposed; Mar 2004, *Aptroot 60644a* (BR, INB). Monte Alto Forest Reserve, 10 km SSE of Nicoya, near Hojancha; 85° 24' W, 10° 00' N, 500 m; lower montane moist forest zone, on trunks in secundary forest around station; Mar 2004, *Sipman 51978, 51998* (B, INB).

***Chapsa meridensis* (Kalb & Frisch) Lücking, Lumbsch & Rivas Plata** (Fig. 8F–H)

Chapsa meridensis (Kalb & Frisch) Lücking, Lumbsch & Rivas Plata in Rivas Plata *et al.*, Lichenologist 42: 183 (2010); *Topeliopsis meridensis* Kalb & Frisch in Frisch & Kalb, Lichenologist 38: 42 (2006). Holotype. Venezuela, *Kalb & López-Figueiras 34793* (hb. Kalb!).

Thallus muscicolous, light grey-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia prominent to sessile, angular-rounded, 0.7–1.2 mm diam.; disc exposed or partly covered, grey-brown, white-grey-pruinose; margin fissured, fused or indistinctly layered, grey-brown, white-pruinose. Columella absent. Excipulum

paraplectenchymatous, brown; periphysoids present. Hymenium 150–200 µm high, inspersed; paraphyses unbranched. Ascospores single, muriform, 100–120 × 20–30 µm, ellipsoid, with slightly thickened septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Chapsa meridensis* is a remarkable species that closely resembles a *Topeliopsis* in ecology and morphology. Molecular data showed that the species belongs in *Chapsa* (Mangold *et al.* 2008b), and this agrees with the apothecia having an exposed disc with erect to recurved lobules when mature, a feature not observed in *Topeliopsis* s.str. (Rivas Plata *et al.* 2010a). Within *Chapsa*, the species is easily identified by its ecology (growing over bryophytes in the subparamo) and *Topeliopsis*-like young apothecia with an inspersed hymenium.

Specimens examined:—COSTA RICA. San José: Los Santos Forest Reserve, Cerro de la Muerte (Pacífico Central Conservation Area), Talamanca Ridge, km 90 on road (ruta 2) from Cartago to San Isidro, access road to towers on summit; 83° 45' W, 9° 34' N, 3400–3500 m; upper montane cloud forest and subalpine paramo zone, disturbed low paramo shrub with Chusquea, on bryophyte, exposed; Mar 2004, *Lücking 17770* (CR, F, INB, USJ).

***Chapsa neei* (Hale) Sipman, Mangold & Lücking** (Fig. 9A)

Chapsa neei (Hale) Sipman, Mangold & Lücking in Rivas Plata *et al.*, Lichenologist 42: 183 (2010); *Ocellularia neei* Hale, Smithson. Contr. Bot. 38: 25 (1978); *Thelotrema neei* (Hale) Hale, Mycotaxon 11: 132 (1980). Holotype. Panama, *Nee & Mori 3710* (US!).

Thallus white-grey, smooth to uneven, ecorticate, endoperidermal; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.4–0.7 mm diam.; disc exposed, purple-brown, white-pruinose; margin entire, with split between thallus and proper margin (double margin), white-grey. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 40–60 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 1–3-septate, 10–14 × 4–6 µm, ellipsoid, with slightly thickened septa and rectangular lumina, brown, I– (non-amyloid). Secondary chemistry: stictic, constictic, hypoconstictic and cryptostictic acids; apothecial disc with purple-brown pigment.

Remarks:—This species resembles a *Thelotrema* rather than *Chapsa*, due to the distinct double margin. A very similar species is *C. platycarpa* (see below), which was confirmed to belong in *Chapsa* by molecular data (Frisch *et al.* 2006). *Chapsa platycarpa* has larger apothecia lacking a purple pigment and the proper excipulum is distinctly lobulate and covers the marginal parts of the disc; also, the young ascospores are amyloid.

Specimens examined:—COSTA RICA. Heredia: La Selva Protection Zone, La Selva Biological Station (Cordillera Volcánica Central Conservation Area), Volcánica Central Ridge, 55 km N of San Jose, access road to station; 84° 03' W, 10° 26' N, 50 m; lowland rain forest zone, trees along main road, on bark (lower stem), fully exposed; Jun 2002, *Lücking 15026e* (F, INB). Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, beach south of station; 83° 36' W, 8° 28' N, sea level; lowland coastal rain forest zone, disturbed coastal forest and exposed trees along beach, on bark (lower stem), semi-exposed; Apr 2003, *Sipman 51108* (B, INB). Osa peninsula, flood plain of Río San Ramón; sea level; Aug–Sep 1936, *Dodge & Goerger 10073* (FH; as *Phaeotrema fuscescens* (Kremp.) Zahlbr.).

Chapsa perdissuta* Sipman & Lücking, *spec. nov. (Fig. 9B)
MycoBank #800074

Differing from *Chapsa dissuta* in the large, muriform ascospores.

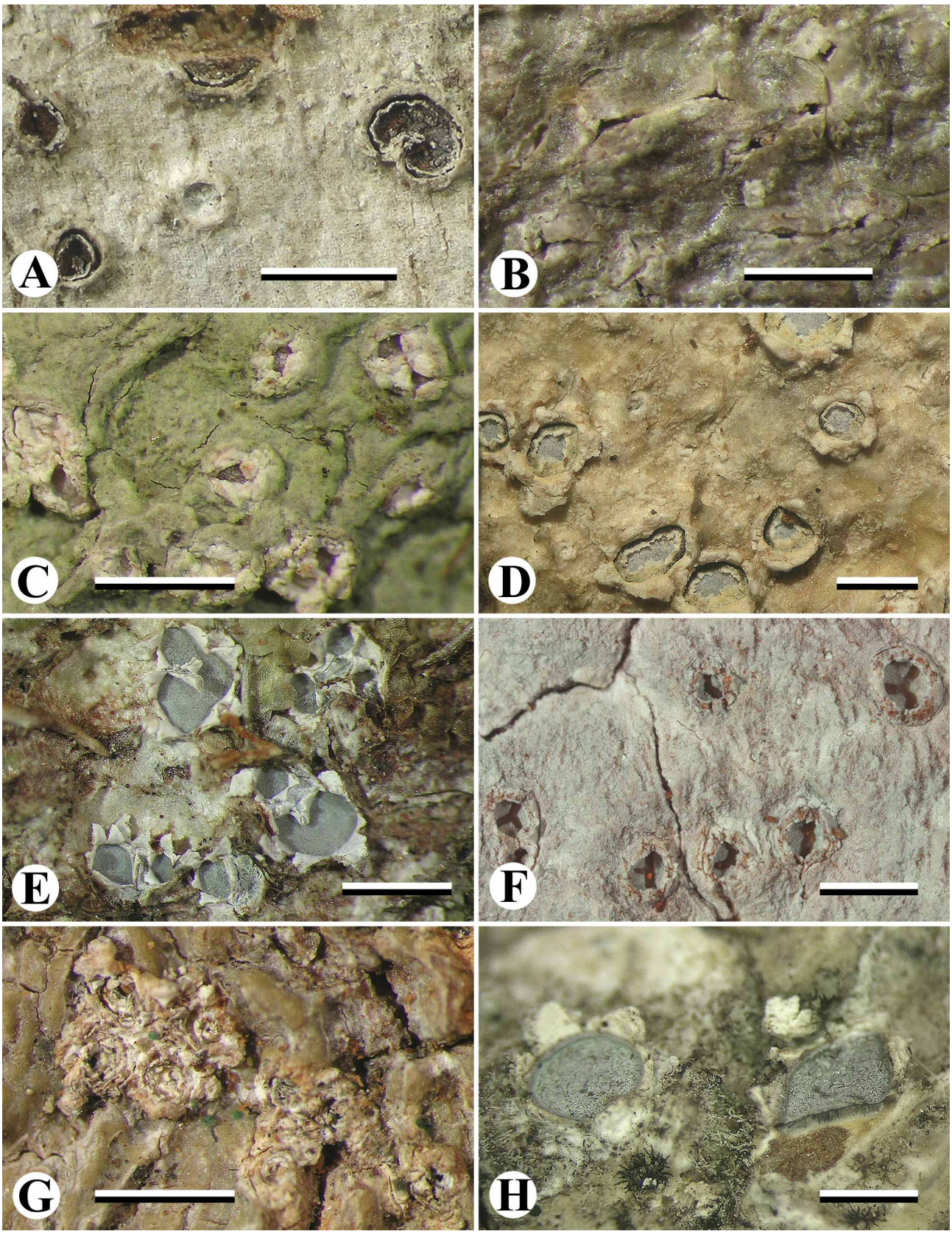

FIGURE 9. A. *Chapsa neei*. B. *Chapsa perdissuta*. C. *Chapsa phlyctidioides*. D. *Chapsa platycarpa*. E. *Chapsa platycarpella*. F. *Chapsa pseudoschizostoma*. G. *Chapsa referta*. H. *Chapsa stellata*. Scale = 1 mm.

Holotype:—COSTA RICA. Puntarenas: Cordillera de Tilaran, Monteverde, near the cheese factory; 84° 49' W, 10° 18' N, 1450 m; premontane rain forest zone, forest relics among pasturefields, on trunks; Jan 1979, *Sipman 12125* (U!).

Thallus light grey-green, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.6–1 mm diam.; disc more or less covered, flesh-colored to pink-brown; margin fissured to lobulate, fused, flesh-colored. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present but mostly found lining the inner and upper part of the thalline margin. Hymenium 200–250 µm high, clear; paraphyses unbranched. Ascospores 1–2/ascus, muriform, 150–180 × 30–40 µm, ellipsoid, with slightly thickened septa and rectangular lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This new species resembles a *Fissurina* but has angular-rounded apothecia and very large ascospores. Its placement in *Chapsa* is provisional and its generic affinities remain obscure. It resembles *C. dissuta* and *C. lassae* (see above) but is clearly set apart by the very large, muriform ascospores.

Additional specimens examined (paratypes):—COSTA RICA. Guanacaste: Volcán Tenorio National Park, Alto Masis Section (Arenal-Tilarán Conservation Area), Tilarán Ridge, 125 km NW of San José, 15 km NNW of Tilarán, near Tierras Morenas, access road to station; 85° 00' W, 10° 36' N, 850–900 m; lower montane moist forest zone, exposed trees and fence posts and forest regrowth along savanna-like pasture, on bark (lower trunk), semi-exposed; Mar 2004, *Lücking 17306* (CR, F, INB, USJ). Puntarenas: Las Cruces Biological Station, San Vito de Coto Brus; 8° 47' N, 82° 58' W, 1200 m; on ridge beyond Rio Java, on trunks and undergrowth of disturbed primary forest; Oct 2004, *Sipman 53253* (B, INB). Puntarenas: Old Camino Real, a few km SE of Paso Real near the Rio Grande de Térraba; 9° 29' N, 84° 09' W, 100 m; tropical rainforest; Dec 1978, *Kalb & Plöbst 38934* (hb. Kalb).

***Chapsa phlyctidioides* (Müll. Arg.) Mangold** (Fig. 9C)

Chapsa phlyctidioides (Müll.Arg.) Mangold in Lumbsch *et al.*, Austral. Syst. Bot. 21: 221 (2008); *Ocellularia phlyctidioides* Müll. Arg., Hedwigia 32: 130 (1893); *Thelotrema phlyctidioides* (Müll.Arg.) Hale, Mycotaxon 11: 132 (1980). Holotype. Australia, *Bailey 354* (G!).

Ocellularia conglomerata Hale, Smithson. Contr. Bot. 16: 19 (1974). Holotype. Lesser Antilles (Dominica), *Hale 37959* (US!).

Thallus light grey-green, smooth to uneven, ecorticate; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.4–0.8 mm diam., often aggregate; disc partially covered, pale brown, white-pruinose; margin lobulate, fused (but excipulum sometimes layered), yellow-white to pale brown, white-pruinose. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 60–80 µm high, clear; paraphyses unbranched, thick, apically moniliform. Ascospores 8/ascus, 5–7-septate, 15–25 × 5–7 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I– (non-amyloid). Secondary chemistry: stictic, constictic, cryptostictic, hypostictic, and α-acetyl-hypoconstictic acids.

Remarks:—*Chapsa phlyctidioides* belongs in the *C. alborosella* aggregate and is most similar to *C. alborosella* (see above), which has apothecia with more or less recurved lobules and lacks secondary substances. The other species in the genus with small, transversely septate ascospores and stictic acid, *C. dilatata* (see above), has a white thallus and large, thickly white-pruinose apothecia with large, erect lobules. *Chapsa phlyctidioides* somewhat resembles a *Thelotrema*, especially apothecia with layered excipulum, but there is no real double margin in this species; the excipulum and thalline margin are fused. The species is found in (lower) montane rain forest in shaded to semi-exposed situations.

Specimens examined:—COSTA RICA. Alajuela: San Ramón Forest Reserve, near house at Río Lorencito, 5 km NE of Cerro Jabonal; 84° 37' W, 10° 13' N, 1000 m; humid, mossy forest with many ferns on

mountain ridge, on thin trunk in undergrowth; Nov 1988, *Sipman et al. 41972* (B, CR), *41974* (B, CR), *41980* (B, CR), *41981* (B, CR). Volcán Tenorio National Park, Pilón Biological Station (Arenal-Tempisque Conservation Area), Tilarán Ridge, 140 km NW of San José, 25 km NNW of Tilarán, near Bijagua, main trail through forest to crater; 84° 59' W, 10° 43' N, 700–900 m; lower montane cloud forest zone, partly disturbed primary forest, on bark (lower stem), partially shaded; Mar 2004, *Lücking 17260* (CR, F, INB), *Aptroot 60496* (BR, INB), *60506* (BR, INB).

***Chapsa platycarpa* (Tuck.) Frisch** (Fig. 9D)

Chapsa platycarpa (Tuck.) Frisch, Biblioth. Lichenol. 92: 113 (2006); *Thelotrema platycarpum* Tuck., Proc. Amer. Acad. Arts Sci. 5: 406 (1862). Holotype. Cuba, *Wright s.n.* (FH!; Wright, Lich. Cub. 139).

Asteristion erumpens Leight., Trans. Linn. Soc. London 27: 163 (1870); *Phaeotrema erumpens* (Leight.) R. Sant., Symb. Bot. Upsal. 12(1): 423 (1952). Lectotype (Hale 1981: 265). Sri Lanka, *Thwaites 5* (BM!; isolectotypes: H-NYL 22683!, S!, UPS!).

Platygrapha alborufa Berk. & Broome, J. Linn. Soc. Bot. 14: 110 (1875); *Cryptodiscus alborufus* (Berk. & Broome) Sacc., Syll. Fung. 8: 674 (1889). Lectotype (Hale 1981: 265). Sri Lanka, *Thwaites 69* (K!).

Phaeotrema apertum C. W. Dodge, Beih. Nova Hedwigia 12: 98 (1964). Holotype. Uganda, *Dümmer 4293* (BM!).

Thallus olive, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia immersed-erumpent, angular-rounded, 1–2.5 mm diam.; disc exposed, grey-brown, white-grey-pruinose; margin lobulate and incurved (proper margin) to recurved (thallus margin), with split between thallus and proper margin (double margin), pale brown, yellowish-white pruinose. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 50–70 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–5-septate, 11–15 × 4–5 µm, fusiform, with thick septa and lens-shaped lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: stictic, constictic, and α-acetyl-constictic acids.

Remarks:—With the large apothecia, contrasting in color between the disc, margin, and thallus, and the proper excipulum forming a veill around the disc, *Chapsa platycarpa* is undoubtely one of the most conspicuous species in the family. It can hardly be confused with any other species in the genus except *C. neei* (see above), which has similar ascospores and chemistry and also features apothecia with a double margin. However, the apothecia are smaller in that species, the disc has a purpish brown pigment, and no excipular veil is developed. The closely related *C. platycarpoides* (Tuck.) Breuss & Lücking has smaller apothecia with UV+ yellow margins (Lücking *et al.* 2011). These species resemble *Thelotrema*, in particular *T. lepadinum* (see below), which also often forms a lobulate excipular veil. However, *Thelotrema* usually has an entire thallus margin. *Chapsa platycarpa* is found predominantly in lowland to montane forests with a distinct dry season and is also a common subtropical species in southern Florida (Lücking *et al.* 2011).

Specimens examined:—COSTA RICA. Cartago: On road Limón-Turrialba, about halfway between Siquirres and Chitaría; 83° 30' W, 10° 03' N, 700 m; on trunks in grazed parkland with groves; Jan 1979, *Sipman 12312* (U). Guanacaste: Monte Alto Forest Reserve, Monte Alto Biological Station (Tempisque Conservation Area), Nicoya Pensinsula, 150 km W of San José, 10 km SSE of Nicoya, near Hojancha, main trails and access road through reserve near station (Sendero Jardín de Orquideas, Sendero Ceiba, Sendero Shannon-Ward); 85° 24' W, 10° 02' N, 450–550 m; lowland to lower montane moist forest zone, disturbed primary and oldgrowth secondary forest, on bark (lower trunk), semi-exposed; Mar 2004, *Aptroot 60781* (BR, INB); ibid., Cerro Romo (Tempisque Conservation Area), Nicoya Pensinsula, 150 km W of San José, 15 km SSE of Nicoya, near Hojancha, access road to Mirador; 85° 24' W, 10° 00' N, 750–900 m; lowland to lower montane moist forest zone, forest regrowth along pasture, on bark (lower trunk), exposed; Mar 2004, *Sipman 52073* (B, INB). Pitilla Biological Station (Guanacaste Conservation Area), on humid E-slope of Volcan Orosi; 85° 26' W, 11° 00' N, 400 m, epiphyte on shrub in clearing near the station; Jun 1995, *Sipman 37279* (B, CR).

***Chapsa platycarpella* (Vain.) Frisch** (Fig. 9E)

Chapsa platycarpella (Vain.) Frisch, Biblioth. Lichenol. 92: 118 (2006); *Thelotrema platycarpellum* Vain., Amer. Acad. Arts Sci. 58: 138 (1923); *Ocellularia platycarpella* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 598 (1923). Holotype. Trinidad and Tobago, *Thaxter 57* (TUR-VAIN 26791!).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex, endoperidermal, often invisible; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.5–1.5 mm diam.; disc exposed, pale brown, white-grey-pruinose with bluish tinge; margin lobulate to recurved, fused, pale brown, white-pruinose. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 40–60 µm high, clear; paraphyses unbranched, thick, apically capitate. Ascospores 8/ascus, 3–5-septate, 10–15 × 4–5 µm, oblong with distal ends tapering, with slightly thickened septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Chapsa platycarpella* is very close to *C. astroidea* (see above) and was synonymized with the latter by Mangold *et al.* (2009). However, in the material studied by us, including abundant collections from Brazil (Cáceres 2007), two forms can be distinguished: one has a distinct, epiperidermal thallus and flesh-colored to pale brown, thinly pruinose apothecia, whereas the other features a thin, often invisible, endoperidermal thallus and grey-pruinose apothecia with bluish tinge and pure white marginal lobules. The type material of *Thelotrema astroideum* fits the first form well and the type of *T. platycarpellum*, although not well developed, represents the second form, and we keep the two separated at the species level. Kalb (2009) described a very similar species, *C. amazonica* Kalb, from Brazil, which appears to differ in very minor anatomical and morphological details from *C. platycarpella*; the relationships between these two species have to be clarified further. *Chapsa platycarpella* is found in wet lowland to montane rain forest, usually on shaded tree trunks.

Specimens examined:—COSTA RICA. Alajuela: Refugio Nacional de Vida Silvestre Mixto Maquenque; 84° 11' W, 10° 42' N, 0–100 m; Apr 2005, *Chaves 2282*, *2393* (INB). Guanacaste: Pitilla Biological Station (Guanacaste Conservation Area), on humid E-slope of Volcan Orosi; 85° 26' W, 11° 00' N, 400 m; epiphyte on shrub in clearing near the station; Jun 1995, *Sipman 37283* (B, CR). Volcán Tenorio National Park, 25 km NNW of Tilarán; 84° 59' W, 10° 43' N, 700–900 m; on tree in disturbed primary forest along trail to waterfall near Bijagua; Mar 2004, *Aptroot 60495* (hb. Aptroot). Puntarenas: San Vito de Coto Brus, Las Cruces Biological Station; 82° 58' W, 8° 47' N, 1200 m; on ridge beyond Río Java, on trunks and undergrowth of disturbed primary forest; Oct 2004, *Sipman 53266* (B, INB).

Chapsa pseudoschizostoma* (Hale) Sipman, *comb. nov. (Fig. 9F)
MycoBank #800061

Ocellularia pseudoschizostoma Hale, Smithson. Contr. Bot. 38: 28 (1978); *Thelotrema pseudoschizostomum* (Hale) Hale, Mycotaxon 11: 132 (1980). Holotype. Panama, *Hale 38559* (US!).

Thallus white-grey-green, smooth to uneven, ecorticate; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.3–0.7 mm diam.; disc exposed, pale brown, white-pruinose, with distinct fissures resembling a pseudocolumella; margin lobulate, fused, pale brown, white-pruinose. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 50–70 µm high, inspersed; paraphyses unbranched. Ascospores 8/ascus, 5–7-septate, 20–25 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, weakly I+ violet-blue (amyloid). Secondary chemistry: stictic and constictic acids.

Remarks:—*Chapsa pseudoschizostoma* is another representative of the *C. alborosella* aggregate and comes closest to *C. dilatata* (see above). However, the inspersed hymenium and the fissured apothecial discs set it apart from all other species of the genus with small, transversey septate ascospores.

Specimens examined:—Not yet found in Costa Rica but reported from Panama (Hale 1978).

Chapsa referta* (Hale) Lücking, *comb. nov. (Fig. 9G)
MycoBank #800062

Ocellularia referta Hale, Smithson. Contr. Bot. 38: 19 (1978); *Thelotrema refertum* (Hale) Hale, Mycotaxon 11: 132 (1980). Holotype: Panama, *Hale 43566* (US!).

Thallus olive-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with scattered clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded to irregular or lobate or sometimes 2–3 confluent, 0.5–0.8 mm diam.; disc covered by 0.2–0.3 mm wide pore and inner layers of excipulum, barely invisible; proper margin fissured to lobulate, yellow-white, layered, laterally covered by thalline layer. Columella absent. Excipulum paraplectenchymatous, apically dark brown; periphysoids present. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–7-septate, 20–25 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids.

Remarks:—This species is here combined in *Chapsa* due to the combination of periphysoids and amyloid ascospores and its similarity with *C. laceratula* and related species (see discussion under that species). The systematic position of these species is preliminary, however (Rivas Plata *et al.* 2010a). In certain aspects they resemble species of *Schizotrema* (differing in the non-carbonized excipulum and amyloid ascospores) and *Topeliopsis* (differing in the thicker, corticate thallus and erumpent apothecia).

Specimens examined:—Not yet known from Costa Rica, but reported from Panama (Hale 1978).

Chapsa stellata* (Hale) Sipman, *comb. nov. (Fig. 9H)
MycoBank #800056

Leptotrema stellatum Hale, Smithson. Contr. Bot. 38: 54 (1978); *Thelotrema stellatum* (Hale) Hale, Mycotaxon 11: 132 (1980). Holotype. Panama, *Hale 44999* (US!).

Thallus light yellow-grey, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 1–2 mm diam.; disc exposed, brown-black, white-pruinose; margin lobulate to recurved, fused, brown-black, white-pruinose. Columella absent. Excipulum paraplectenchymatous, brown; periphysoids present. Hymenium 150–220 µm high, clear; paraphyses unbranched. Ascospores 2/ascus, 100–120 × 20–25 µm, oblong, with thick septa and lens-shaped lumina, brown, I– (non-amyloid), richly muriform. Secondary chemistry: no substances detected by TLC.

Remarks:—*Chapsa stellata* resembles a *Phaeographis* with rounded apothecia, such as *P. lobata* (Eschw.) Müll. Arg., but anatomically can be identified as *Chapsa* due to the lateral periphysoids. Within *Chapsa*, it is the only species known with large muriform, brown ascospores.

Specimens examined:—Not yet found in Costa Rica but reported from Panama (Hale 1978).

***Chapsa sublilacina* (Ellis & Everh.) M. E. S. Cáceres & Lücking** (Fig. 10A–B)

Chapsa sublilacina (Ellis & Everh.) M. E. S. Cáceres & Lücking in Cáceres, Libri Bot. 22: 54 (2007); *Chapsa sublilacina* (Ellis & Everh.) Sipman & Lücking in Rivas Plata et al., Lichenologist 42: 153 (2010), comb. inval.; *Karstenia sublilacina* Ellis & Everh. in Smith, Centr. Amer. Fungi, no. 49; Bull. Labs Nat. Hist. St. Univ. Ia(4): 69 (1896); *Thelotrema sublilacinum* (Ellis & Everh.) Vain., Proc. Amer. Acad. Arts Sci. 58: 137 (1923). Lectotype (Hale 1978: 31). Nicaragua, *Smith 49* (BPI!).

Thallus olive-green, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer with scattered clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 1–3(–5) mm diam.; disc exposed, flesh-colored to pink-purple; margin lobulate to recurved, often layered, flesh-colored to beige. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 150–200 µm high, clear; paraphyses unbranched. Ascospores 2–4/ascus, 15–19-septate, 60–120 × 10–15 µm, cylindrical, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: stictic, constictic, hypoconstictic and cryptostictic acids.

Remarks:—*Chapsa sublilacina* forms the center of a group of rain forest understory species with large, compact, corticate thallus, large apothecia with flesh-colored to purplish disc, and large, transversely septate, amyloid ascospores. The common non-sorediate form with stictic acid bears the name *C. sublilacina*, but three other species and one variety are described here differing in the presence and type of soralia and in secondary chemistry: *C. defecta* (non-sorediate, no substances), *C. defectosorediata* (sorediate with scattered soralia, no substances), *C. thallotrema* (sorediate with large, capitate soralia, stictic acid), and *C. sublilacina var. cyanea* (with blue apothecial disc).

Specimens examined:—COSTA RICA. Alajuela: Maquenque Mixed National Wildlife Refuge, Huetar Norte; 84° 11' W, 10° 42' N, 0–100 m; Apr 2005, *Chaves 2261* (INB). Guanacaste: Miravalles Protection Zone, Cerro La Giganta; 85° 07' W, 10° 41' N, 900–1000 m; Jan 2005, *Rodríguez 377* (INB). Pitilla Biological Station (Guanacaste Conservation Area), on humid E-slope of Volcán Orosi; 85° 26' W, 11° 00' N, 500 m; epiphyte in relic of primary forest near the station; Jun 1995, *Sipman 37285* (B, CR). Upper portion of cañon of Río San José; 680–780 m; Dec 1930, *Dodge & Thomas 6894* (FH; as *Ocellularia crispata* Müll. Arg.). Limón: Hitoy Cerere Biological Reserve, near Pandora, 40 km S of Limón; 83° 02' W, 9° 40' N, 150–500 m; on tree in disturbed primary forest along trail; Mar 2004, *Aptroot 60224* (hb. Aptroot). Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, trail S of station to Río Claro; 83° 35' W, 8° 28' N, 0–100 m; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants, on bark (lower trunk), semi-exposed; Apr 2003, *Nelsen 3573e* (INB, WIS); ibid., round trail NW of station (Sendero Sirena and Sendero Guanacaste); 83° 35' W, 8° 29' N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (lower stem), partially shaded; Apr 2003, *Grube 11490* (GZU, INB), *Lücking 16218d*, *16224b* (F, INB), *Sipman 51162b*, *51164*, *51168* (B, INB); ibid., on bark (lower trunk), partially shaded; Apr 2003, *Lücking 16214* (CR, F, INB, USJ), *16239* (F, INB). Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), partially shaded; Feb 1997, *Lücking 97-248* (F). Monte Verde, Cordillera de Tilaran, ca. 20 km E of Juntas; Jan 1979, *Filson 16349* (MEL).

Chapsa sublilacina* var. *cyanea* Lücking, *var. nov. (Fig. 10C–E)
MycoBank #800105

Differing from var. *sublilacina* in the bluish pruinose apothecial disc.

Holotype:—COSTA RICA. Guanacaste: 8.5 km E of Guayabos on the lower slopes of Miravalles volcano (Guayabos is 25 km E of Bagaces on the Interamerica Hwy.); Jan 1979, *Filson 16475* (MEL).

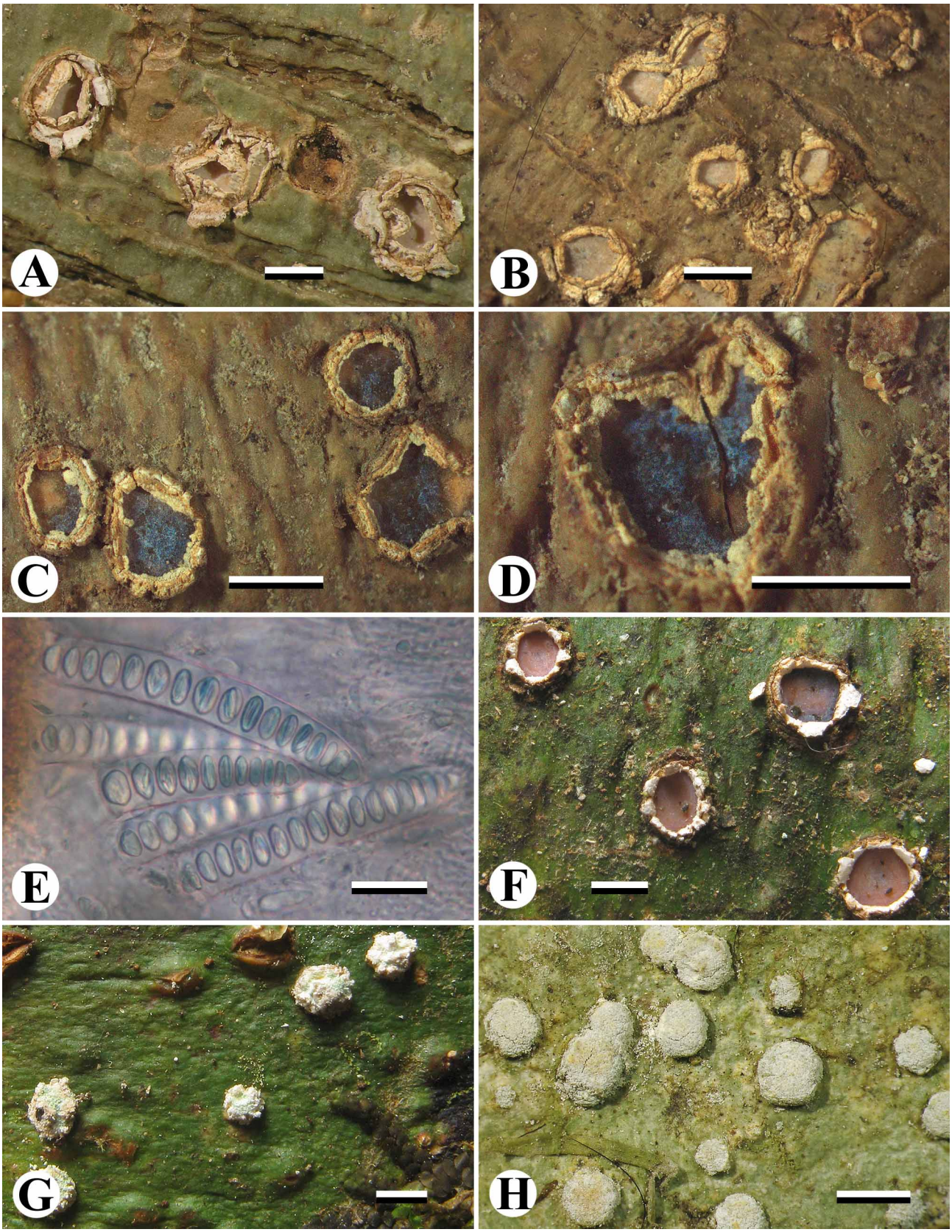

FIGURE 10. A–B. *Chapsa sublilacina*. C–E. *Chapsa sublilacina var. cyanea*. F–H. *Chapsa thallotrema*. Scale = 1 mm.

Thallus olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer with scattered clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 1–3 mm diam.; disc exposed, appearing bluish due to a pruinose layer; margin lobulate to recurved, layered, flesh-colored to beige. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 150–200 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 19–25-septate, 80–130 × 12–16 µm, cylindrical, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: stictic, constictic, hypoconstictic and cryptostictic acids.

Remarks:—This variety differs from all known collections of the nominal variety by the bluish pruina on the disc surface. Typical *Chapsa sublilacina* is epruinose and the disc is flesh-colored to pink-purple. The blue color of the apothecial pruina appears to be a physical effect of the crystals forming the pruina, very much like in the foliicolous lichen, *Arthonia cyanea* Müll. Arg. (Lücking 2008). *Chapsa sublilacina* var. *cyanea* was found in northwestern parts of Costa Rica in the Cordillera de Tilarán, whereas the nominal variety occurs in the rain forests of the Atlantic and southern Pacific sides. The new variety also seems to differ by the 8-spored asci. Pending further study on this aberrant population, we considered it most appropriate to give it the rank of variety because of its restricted distribution.

Chapsa thallotrema **Lücking & N. Salazar** (Fig. 10F–H)

Chapsa thallotrema Lücking & N. Salazar in Lumbsch *et al.*, Phytotaxa 18: 39 (2011). Holotype: Panama, *Lücking 27305* (F!; isotype: PMA!).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting, sorediate; soralia scattered, round, distinctly capitate, 0.7–1.2 mm wide, white to pale blue-grey; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 1–3(–5) mm diam.; disc exposed, flesh-colored to pink-purple; margin lobulate to recurved, often layered, flesh-colored to beige. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 150–200 µm high, clear; paraphyses unbranched. Ascospores 2–4/ascus, 15–19-septate, 60–120 × 10–15 µm, cylindrical, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: stictic, constictic, hypoconstictic and cryptostictic acids.

Remarks:—This species is close to *Chapsa sublilacina* (see above), but differs in the conspicuous soralia and can be considered the sorediate counterpart of the latter. Preliminary molecular data suggest that the two are not conspecific (Rivas Plata *et al.*, unpubl.). *Chapsa thallotrema* is a common and widespread species on trunks in primary tropical forestm but so far it was known only in the sterile state. In the absence of ascocarps, it had been provisionally named '*Thallotrema antillarum*' on herbarium specimens by the research group of Henry Imshaugh. This name was never published and the epithet was choosen in honour of the excellent collecting activities of this group (Lumbsch *et al.* 2011). *Chapsa thallotrema* is a common lowland to montane rain forest species on shaded tree trunks.

Specimens examined:—COSTA RICA. Alajuela: Volcán Tenorio National Park, Pilón Biological Station (Arenal-Tempisque Conservation Area), Tilarán Ridge, 140 km NW of San José, 25 km NNW of Tilarán, near Bijagua, access road to station and river; 84° 59' W, 10° 43' N, 700 m; lower montane cloud forest zone, exposed trees and fence posts along pasture, on bark (lower stem), partially shaded; Mar 2004, *Nelsen 3745* (INB, WIS), *Lücking 17219* (F); ibid., main trail through forest to crater; 84° 59' W, 10° 43' N, 700–900 m; lower montane cloud forest zone, partly disturbed primary forest, on bark (branch), semi-exposed; Mar 2004, *Will-Wolf 12745b* (CR, INB, WIS). Limón: Hitoy Cerere Biological Reserve, 40 km S of Limón, forest trail above station, along Espavel trail; 9° 40' N, 83° 02' W, 300 m; submontane rain forest zone, on trunks in disturbed primary forest; Mar 2004, *Sipman 51631* (B, INB). Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, round trail NW of station (Sendero Sirena and Sendero Guanacaste); 83° 35' W, 8° 29'

N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (lower stem), partially shaded; Apr 2003, *Lücking 16204* (F, USJ); ibid., on bark (lower trunk), partially shaded; Apr 2003, *Lücking 16228* (F, INB).

Chroodiscus Müll. Arg.

Thallus smooth to uneven or distinctly verrucose, with cartilaginous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded or lobate-lirellate; disc exposed, grey to grey-brown or scarlet-red; margin lobulate to recurved, white-grey or yellow-orange. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids absent. Paraphyses unbranched, thick, apically capitate. Ascospores 8/ascus, ellipsoid, with thin septa and rectangular lumina, I– (non-amyloid), 1-septate to submuriform. Secondary chemistry: stictic acid and satellites sometimes present, apothecial disc sometimes with anthraquinones.

Remarks:—The genus *Chroodiscus*, previously only including foliicolous taxa (Santesson 1952), had been emended to include corticolous species with chroodiscoid apothecia (Kalb 1991; Vězda 1992; Kantvilas & Vězda 2000). However, Frisch (2006) retained *Chroodiscus* in its traditional sense and placed most corticolous species in *Chapsa*. This has been confirmed by molecular data (Papong *et al.* 2009a).

Key to the species of *Chroodiscus* found in Costa Rica (5)

1. Apothecial disc scarlet-red 2
- Apothecial disc grey 4

2. Ascospores 1-septate; thallus smooth to uneven; photobiont *Trentepohlia*-like, leaving interspaces between threads. ..... ***C. australiensis***
- Ascospores 3-septate or submuriform; thallus distinctly verrucose; photobiont *Phycopeltis*, with closed, radiating plates 3

3. Ascospores 3-septate ..... ***C. coccineus***
- Ascospores submuriform ..... ***C. submuralis***

4. Ascospores 1-septate; thallus distinctly verrucose; photobiont *Phycopeltis*, with closed, radiating plates ..... ***C. neotropicus***
- Ascospores 3-septate; thallus smooth to uneven; photobiont *Trentepohlia*-like, leaving interspaces between threads. ..... ***C. argillaceus***

Chroodiscus argillaceus (Müll. Arg.) Lücking & Papong (Fig. 11A)

Chroodiscus argillaceus (Müll. Arg.) Lücking & Papong, Bryologist 112: 154 (2009); *Ocellularia argillacea* Müll. Arg., Flora 66: 352 (1883). Holotype. Malaysia (Borneo), *Beccari 687* (G!).
Ocellularia argillacea var. *radians* Müll. Arg., Flora 66: 352 (1883). Holotype. Malaysia (Borneo), *Beccari 3647* (G!).
Chroodiscus parvisporus Kalb & Lücking in Lücking & Grube, Stapfia 80: 271 (2002). Holotype. Australia, *Kalb & Kalb s.n.* (hb. Kalb!).

Thallus light grey-green, smooth to uneven, with cartilaginous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.2–0.6 mm diam.; disc exposed, grey; margin fused, lobulate to recurved, white-grey. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids absent. Hymenium 40–60 µm high, clear; paraphyses unbranched, thick, apically capitate. Ascospores 8/ascus, 3-septate, 8–10 × 2.5–3.5 µm, ellipsoid, with thin septa and rectangular lumina, I– (non-amyloid). Secondary chemistry: stictic acid.

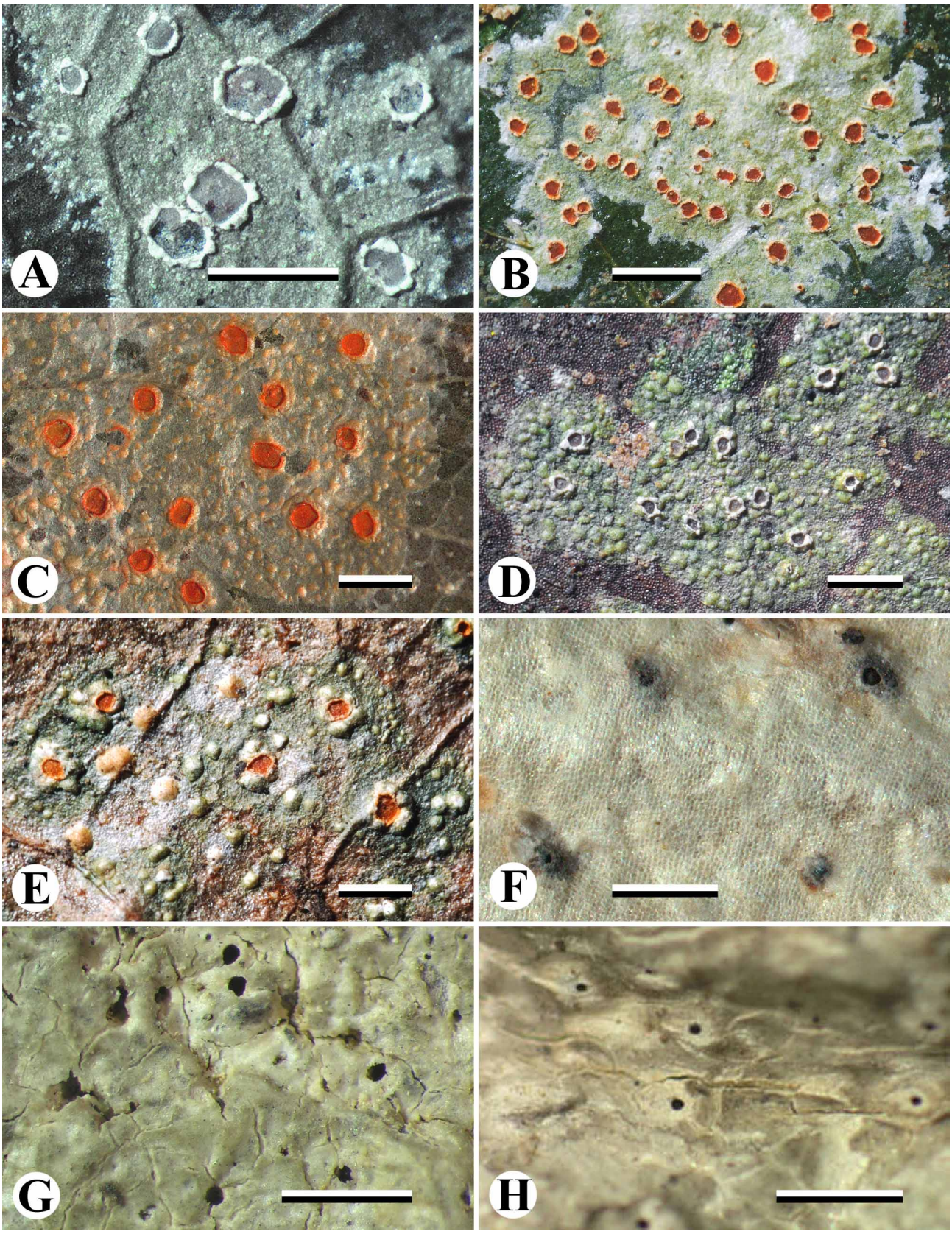

FIGURE 11. A. *Chroodiscus argillaceus*. B. *Chroodiscus australiensis*. C. *Chroodiscus coccineus*. D. *Chroodiscus neotropicus*. E. *Chroodiscus submuralis*. F. *Clandestinotrema analorenae*. G. *Clandestinotrema antoninii*. H. *Clandestinotrema clandestinum*. Scale = 1 mm.

Remarks:—This species belongs in the early diverging group of the genus, together with the palaeotropical *C. mirificus* (Kremp.) R. Sant. and relatives (Lücking *et al.* 2008c; Papong *et al.* 2009b). It was described as *C. parvisporus* from Australia (Lücking & Grube 2002), but revision of the putative synonyms of *C. mirificus* (Santesson 1952) revealed *argillaceus* as an earlier epithet (Papong *et al.* 2009b).

Specimens examined:—COSTA RICA. Puntarenas: Cocos Island National Park, Wafer Bay; 1992, *Lücking 1033* (F).

***Chroodiscus australiensis* Vězda & Lumbsch** (Fig. 11B)

Chroodiscus australiensis Vězda & Lumbsch in Lumbsch & Vězda, Nova Hedwigia 50: 246 (1990). Holotype. Australia, *Lumbsch 5437ei* (F!; isotype: hb. Vězda!).

Thallus light grey-green, smooth to uneven, with cartilaginous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.15–0.3 mm diam.; disc exposed, scarlet-red; margin fused, lobulate to recurved, orange to scarlet-red. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids absent. Hymenium 40–50 µm high, clear; paraphyses unbranched, thick, apically capitate. Ascospores 8/ascus, 1-septate, 7–10 × 2–2.5 µm, ellipsoid, with thin septa and rectangular lumina, I– (non-amyloid). Secondary chemistry: stictic acid, apothecial disc with orange-red (K+ purple) anthraquinone.

Remarks:—*Chroodiscus australiensis* is the most widely distributed species of the genus (Lücking *et al.* 2008b). Its photobiont is morphologically different from that of other species of the genus (Lücking & Grube 2002) but molecular phylogenetic analyses show that photobiont morphology plays only a minor role in defining clades within the Trentepohliaceae (Nelsen *et al.* 2011).

Specimens examined:—COSTA RICA. Cartago: CATIE agricultural research centre near Turrialba, Los Espaveles natural trail; 9° 55' N, 83° 40' W, 600 m; foliicolous in undergrowth of primary forest on steep slope along river; Nov 1988, *Sipman & Döbbeler 42421* p.p. (B, CR). See also Lücking (1999, 2008).

***Chroodiscus coccineus* (Leight.) Müll. Arg.** (Fig. 11C)

Chroodiscus coccineus (Leight.) Müll. Arg., Lich. Epiphylli Novi: 18 (1890); *Platygrapha coccinea* Leight., Trans. Linn. Soc. 25: 456 (1866); *Thelotrema coccineum* (Leight.) Hale, Bull. Br. Mus. Nat. Hist. (Bot.) 8: 253 (1981). Lectotype (Santesson, 1952: 309). Brazil, *Spruce 443* (BM ex K!; isolectotype: UPS!).
Platygrapha rutila Stirt., Proc. Roy. Phil. Soc. Glasgow 11: 104 (1878). Lectotype (Santesson, 1952: 309). Brazil, *Trail s.n.* (BM ex K!; isolectotype: G!).
Chroodiscus igneus Müll. Arg., Lich. Epiphylli Novi: 19 (1890). Holotype. Brazil, *Spruce 2309* (G!).

Thallus light grey-green, verrucose, with cartilaginous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.2–0.4 mm diam.; disc exposed, scarlet-red; margin fused, lobulate to recurved, orange to scarlet-red. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids absent. Hymenium 40–60 µm high, clear; paraphyses unbranched, thick, apically capitate. Ascospores 8/ascus, 3-septate, 8–12 × 2.5–4 µm, ellipsoid, with thin septa and rectangular lumina, I– (non-amyloid). Secondary chemistry: no substances detected by TLC, apothecial disc with orange-red (K+ purple) anthraquinone.

Remarks:—*Chroodiscus coccineus* is one of the most conspicuous and prettiest of foliicolous lichens (Lücking 2008). It is quite abundant in the Neotropics and the possible number of individuals across its range was estimated in the trillions (Lücking *et al.* 2008b). Locally deviating forms with submuriform ascospores or with lobate-lirellate apothecia have been recognized as separate species (Lücking 2008). The species often grows as juvenile parasite on species of the *Porina epiphylla* group (Lücking & Grube 2002).

Specimens examined:—COSTA RICA. Alajuela: San Ramón Forest reserve, near house at Río Lorencito, 5 km NE of Cerro Jabonal; 10° 13' N, 84° 37' W, 1000 m; humid, mossy forest with many ferns on mountain ridge, foliicolous in undergrowth; Nov 1988, *Sipman et al. 42033a* (B, CR). Limón: Margin of Bonilla Lakes above tunnel camp; 300–430 m; Dec 1929, *Dodge et al. s.n.* (FH). See also Lücking (1999, 2008).

***Chroodiscus neotropicus* Kalb & Vězda** (Fig. 11D)

Chroodiscus neotropicus Kalb & Vězda, Nova Hedwigia 55: 199 (1992). Holotype. Brazil, *Kalb & Plöbst s.n.* (hb. Kalb!; isotype: hb. Vězda!).
Chroodiscus santessonii Lücking, Nova Hedwigia 52: 291, 303 (1991); nom. inval., ICBN Art. 34. Original material. Costa Rica, *Lücking 726* (F!).

Thallus light grey-green, verrucose, with cartilaginous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.15–0.25 mm diam.; disc exposed, grey-brown; margin fused, lobulate to recurved, white-grey. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids absent. Hymenium 40–50 µm high, clear; paraphyses unbranched, thick, apically capitate. Ascospores 8/ascus, 1-septate, 6–10 × 2–2.5 µm, ellipsoid, with thin septa and rectangular lumina, I– (non-amyloid). Secondary chemistry: stictic acid.

Remarks:—*Chroodiscus neotropicus* belongs in a group of species with the same thallus morphology but different ascospore size and septation, and it appears that these species show a vicariant distribution pattern in the Neotropics and Palaeotropics (Lücking *et al*. 2008b). All neotropical populations have 1-septate ascospores and represent *C. neotropicus*, whereas African populations have larger, 3-septate ascospores, and belong to *C. verrucosus* R. Sant., Lücking & Vězda. A third species with 5-septate ascospores, *C. khaolungensis* Papong & Lücking, was described from Thailand (Papong *et al.* 2009b).

Specimens examined:—Costa Rica. Heredia. La Selva Biological Station; lowland rain forest; Sep 1991, *Lücking 91-5189* (F); ibid., Apr 1997, *Lücking 97-590* (USJ), 97-1357 (CR), *97-1683* (INB). See also Lücking (1999, 2008).

***Chroodiscus submuralis* Lücking** (Fig. 11E)

Chroodiscus submuralis Lücking, Cryptog. Mycol. 20: 215 (1999). Holotype. Costa Rica, *Lücking 91-3560* (CR!; isotypes: B!, LG!).

Thallus light grey-green, verrucose, with cartilaginous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.3–0.5 mm diam.; disc exposed, scarlet-red; margin fused, lobulate to recurved, orange to scarlet-red. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids absent. Hymenium 50–60 µm high, clear; paraphyses unbranched, thick, apically capitate. Ascospores 8/ascus, submuriform with 3–5 transverse and 0–1 longitudinal septa per segment, 12–16 3.5–5 µm, ellipsoid, with thin septa and rectangular lumina, I– (non-amyloid). Secondary chemistry: no substances detected by TLC, apothecial disc with orange-red (K+ purple) anthraquinone.

Remarks:—This rare and easily overlooked species is closely related to *Chroodiscus coccineus* (see above) and differs only in the slightly larger, submuriform ascospores.

Specimens examined:—COSTA RICA. Cartago: CATIE agricultural research centre near Turrialba, Los Espaveles natural trail; 9° 55' N, 83° 40' W, 600 m; foliicolous in undergrowth of primary forest on steep slope along river; Nov 1988, *Sipman & Döbbeler 42421* p.p. (B, CR). See also Lücking (1999, 2008).

Clandestinotrema Rivas Plata, Lumbsch & Lücking

Clandestinotrema Rivas Plata, Lumbsch & Lücking in Rivas Plata *et al.*, Fungal Diversity 52: 116 (2011). Type. *Clandestinotrema clandestinum* (Ach.) Rivas Plata, Lumbsch & Lücking.

Thallus white-grey to yellow-grey, smooth to uneven, ecorticate or with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed to erumpent, rounded to angular; disc usually covered by narrow pore and filled by brown-black, often white-pruinose columella; margin entire to fissured-lobulate, fused, brown-black. Columella usually present, mostly carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Paraphyses unbranched. Ascospores usually 8/ascus, 3-septate to muriform, ellipsoid, with thick septa and diamond-shaped lumina (*Astrothelium*-like), when young central septum becoming thickened before further septa appear (looking *Caloplaca*-like), colorless, I– (non-amyloid). Secondary chemistry: no substances or stictic acid and satellites.

Remarks:—*Clandestinotrema* is a recent segregate of *Ocellularia* and also includes some species previously placed in *Thelotrema* (Rivas Plata *et al.* 2012a). It corresponds to the *Ocellularia clandestina* group as defined by Frisch (2006). Its characteristic feature is the *Astrothelium*-like ascospores, which are otherwise found in the family only in the genera *Cruentotrema* (see below) and *Dyplolabia* and some species of *Fissurina*. Phylogenetic analysis shows that these genera are closely related, very distant from the bulk of the former Thelotremataceae but close to *Fissurina* (Rivas Plata & Lumbsch 2011a). This comes as a surprise since morphologically, species of *Clandestinotrema* closely resemble representatives of the *Ocellularia* clade, such as *O. pyrenuloides* and *Melanotrema meiospermum* (Frisch 2006; Frisch & Kalb 2006; Rivas Plata *et al.* 2012a). *Clandestinotrema* is also ecologically distinct as its species occur, contrary to most other thelotremoid Graphidaceae, principally at high altitudes in wet cloud forests with abundant bryophyte growth.

Key to the species of *Clandestinotrema* found in Costa Rica (9)

1. Apothecial pore wide (0.2–0.5 mm), filled by broad-stump-shaped columella; margin entire to fissured; thallus ecorticate 2
- Apothecial pore narrow (0.05–0.2 mm), filled by narrow, finger-like columella or columella absent; margin entire; thallus with loose to dense cortex 5

2. Stictic acid 3
- No substances 4

3. Ascospores 15–25 × 6–10 µm, submuriform; excipulum laterally carbonized ..... ***C. stylothecium***
- Ascospores 35–45 × 15–20 µm, muriform; excipulum apically carbonized ..... ***C. cathomalizans***

4. Ascospores 15–25 × 6–10 µm, submuriform ..... ***C. pauperius***
- Ascospores 25–40 × 10–17 µm, muriform ..... ***C. leucomelaenum***

5. Ascospores 25–50 × 10–20 µm; columella absent; stictic acid 6
- Ascospores 10–25 × 5–10 µm; columella present or absent in part of the apothecia; no substances or stictic acid 7

6. Ascospores 35–50 × 15–20 µm; cortex loose, irregular ..... ***C. erumpens***
- Ascospores 25–45 × 10–15 µm; cortex dense, prosoplectenchymatous ..... ***C. antoninii***

7. Ascospores 3-septate; stictic acid; excipulum carbonized ..... ***C. analorenae***
- Ascospores submuriform; chemistry and excipulum variable 8

8. Excipulum carbonized; stictic acid ..... ***C. clandestinum***
- Excipulum (apically) dark brown; no substances ..... ***C. tenue***

Clandestinotrema analorenae* Lücking, *spec. nov. (Fig. 11F)
MycoBank #800075

Differing from *Clandestinotrema maculatum* in the carbonized excipulum.

Holotype:—COSTA RICA. Cartago: Tapantí National Park, Tapantí Section, Tapantí Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 35 km SE of San José and 18 km SE of Cartago, trail above road (Sendero Árboles Caidos); 83° 47' W, 9° 45' N, 1400–1600 m; montane rain forest zone, closed primary forest and roadside, on bark (branch), partially shaded; Apr 2003, *Lücking 16569* (INB).

Thallus white-grey, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.2–0.3 mm diam.; disc covered by narrow, 0.05–0.1 mm wide pore, filled by brown-black columella; margin entire, fused, brown-black. Columella present, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3-septate, 12–16 × 5–7 µm, ellipsoid, with thick septa and diamond-shaped lumina (*Astrothelium*-like), colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This new species is similar to *Clandestinotrema clandestinum* (see below), *C. maculatum* (Hale) Rivas Plata, Lücking & Lumbsch, and *C. tenue* (see below). The latter two have a dark brown (uncarbonized) excipulum but *C. maculatum* otherwise agrees in ascospores and chemistry. *Clandestinotrema clandestinum* is superficially similar and also has a carbonized excipulum but differs in its submuriform ascospores and the presence of stictic acid from *C. analorenae*. The new species is dedicated to Ana Lorena Guevara, former director of INBio.

***Clandestinotrema antoninii* (Purvis & P. James) Rivas Plata, Lücking & Lumbsch** (Fig. 11G)

Clandestinotrema antoninii (Purvis & P. James) Rivas Plata, Lücking and Lumbsch in Rivas Plata *et al.*, Fungal Diversity 52: 118 (2011); *Thelotrema antoninii* Purvis & P. James in Purvis *et al.*, Biblioth. Lichenol. 58: 341 (1995). Holotype. Portugal (Azores), *Purvis & James 1993* (BM!).

Thallus white-grey, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed-erumpent, rounded, 0.5–0.8 mm diam.; disc covered by 0.1–0.2 mm wide pore; margin entire to sometimes slightly fissured, white-grey to darkened. Columella absent. Excipulum prosoplectenchymatous, upper half carbonized; periphysoids absent. Hymenium 90–130 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, muriform, 25–45 × 10–25 µm, ellipsoid, with thick septa and diamond-shaped lumina (*Astrothelium*-like), colorless, I– (non-amyloid). Secondary chemistry: stictic, constictic, hypostictic, and menegazziaic acids.

Remarks:—This species was described from the Azores, but the present material fits the type collection remarkably well, fulfilling the prediction by the original authors (Purvis & James 1995) that it would eventually be found in the Neotropics. *Clandestinotrema antoninii* is similar to *C. clandestinum* (see below), but the latter has a columella at least in part of the apothecia and the ascospores are distinctly smaller. Also similar is *C. erumpens* (see below), which differs in the loose cortex and slightly larger (broader) ascospores.

Specimens examined:—COSTA RICA. San José: Cordillera de Talamanca, Interamerican Highway near El Empalme, S side of the highway to San Pablo; 9° 13' N, 83° 37' W, 2200 m; lower mountain rainforest; Dec 1978, *Kalb & Plöbst 38947* (hb. Kalb).

Clandestinotrema cathomalizans (Nyl.) Rivas Plata, Lücking & Lumbsch

Clandestinotrema cathomalizans (Nyl.) Rivas Plata, Lücking & Lumbsch in Rivas Plata *et al.*, Fungal Diversity 52: 118 (2011); *Thelotrema leucomelaenum* var. *cathomalizans* Nyl., Acta Soc. Sci. Fenn. 7: 452 (1863). Lectotype (Hale 1978: 43). Colombia, *Lindig s.n.* (H-NYL 22581!; isolectotypes: BM!, FH!).

Thallus white-grey, smooth to uneven, ecorticate; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.4–0.8 mm diam.; disc partially covered by 0.2–0.4 mm wide pore which is filled by brown-black, white-pruinose columella; margin fissured, fused, brown-black. Columella present, broad-stump-shaped, carbonized. Excipulum prosoplectenchymatous, apically carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, muriform, 35–45 × 15–20 µm, ellipsoid, with thick septa and diamond-shaped lumina (*Astrothelium*-like), colorless, I– (non-amyloid). Secondary chemistry: stictic, constictic, hypoconstictic and cryptostictic acids.

Remarks:—This species was tentatively considered a synonym of *Clandestinotrema clandestinum* by Frisch (2006), who noticed its morphological similarity with *C. leucomelanum* (which lacks stictic acid) but was not aware that there are several distinct species with this type of morphology. *Clandestinotrema cathomalizans* is distinguished from the closely related *C. stylothecium* (see below) by the larger ascospores and the more or less apically carbonized excipulum. Intermediate forms appear to be rare. It agrees with *C. leucomelaenum* (see below) in ascospore size and septation but the latter lacks stictic acid.

Specimens examined:—COSTA RICA. Cartago: Río Macho Forest Reserve, La Chonta, 5 km S of El Empalme on road to San Isidro del General; 83° 56' W, 9° 42' N, 2300 m; fence posts and forest relics in pasture fields on mountain ridge; Nov 1988, *Sipman et al. 41747* (B, CR). Guanacaste: Volcán Tenorio National Park, 25 km NNW of Tilarán; 84° 59' W, 10° 43' N, 700 m; on tree in meadow along access road to station near Bijagua; Mar 2004, *Aptroot 60543* (hb. Aptroot). Volcán Tenorio National Park, 15 km NNW of Tilarán, Alto Masis; 85° 00' W, 10° 37' N, 950–1000 m; on tree in disturbed elfin forest near Tierras Morenas; Mar 2004, *Aptroot 60597* (hb. Aptroot).

Clandestinotrema clandestinum (Ach.) Rivas Plata, Lücking & Lumbsch (Fig. 11H)

Clandestinotrema clandestinum (Ach.) Rivas Plata, Lücking & Lumbsch in Rivas Plata *et al.*, Fungal Diversity 52: 118 (2011); *Ocellularia clandestina* (Ach.) Müll. Arg., Mém. Soc. Phys. Hist. Nat. Genève 29(8): 7 (1887); *Pyrenula clandestina* Ach., Ges. Naturforsch. Freunde Berliner Magazin 6: 10 (1814); *Sphaeromphale clandestinum* (Ach.) Trevis., Conspectus Verrucarianum: 7 (1860); *Thelotrema acharianum* Salisb., Nova Hedwigia 29: 413 (1978) [nom. nov. pro *Pyrenula clandestina* Ach., non *Thelotrema clandestinum* Fée]. Lectotype (Hale 1972: 190). America meridionali, s.col. (S!; isolectotypes: H-ACH 806!, UPS!).

Thelotrema laevigans Nyl., Acta Soc. Sci. Fenn. 7: 451 (1863); *Ocellularia laevigans* (Nyl.) Hale, Mycotaxon 11: 137 (1980). Lectotype (Hale 1978: 43). Colombia, *Lindig 893* (BM!; isolectotypes: FH!, G!, H-NYL 3883! p.p.).

Thelotrema laevigans f. *avertens* Nyl., Ann. Sci. Nat. Bot., Sér. 5, 7: 318 (1867). Holotype. Colombia, *Lindig 134* (H-NYL 22606!; isotypes: BM!, G!, FH!, M!, W!).

Thallus light grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.2–0.4 mm diam.; disc covered by narrow, 0.05–0.2 mm wide pore, filled by brown-black columella; margin entire, brown. Columella partly present, apically carbonized. Excipulum prosoplectenchymatous, apically carbonized; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–1 longitudinal septa per segment, 16–23 × 7–9 µm, ellipsoid, with thick septa and diamond-shaped lumina (*Astrothelium*-like), colorless, I– (non-amyloid). Secondary chemistry: stictic, constictic, cryptostictic, and hypostictic acids, sometimes norstictic acid in trace amounts.

Remarks:—*Clandestinotrema clandestinum* (not to be confused with *Myriotrema clandestinum*; see below) is the type species of the genus (Rivas Plata *et al.* 2012a). Its distinctiveness was first recognized by

Frisch (2006). It is most similar to *C. tenue* (see below), which has a dark brown excipulum and lacks lichen substances, and *C. analorenae* (see above), which has 3-septate ascospores and also lacks lichen substances.

Specimens examined:—COSTA RICA. Guanacaste: Volcán Tenorio National Park, 15 km NNW of Tilarán, Alto Masis; 85° 00' W, 10° 37' N, 950–1000 m; on tree in disturbed elfin forest near Tierras Morenas; Mar 2004, *Aptroot 60624* (hb. Aptroot). San José: Cordillera de Talamanca, Interamerican Highway near El Empalme, S side of the highway to San Pablo; 9° 13' N, 83° 37' W, 2200 m; lower mountain rainforest; Dec 1978, *Kalb & Plöbst 38937*, *38939*, *38940* (hb. Kalb).

Clandestinotrema erumpens **(H. Magn.) Rivas Plata, Lücking & Lumbsch** (Fig. 12A)

Clandestinotrema erumpens (Magn.) Rivas Plata, Lücking & Lumbsch in Rivas Plata *et al.*, Fungal Diversity 52: 118 (2011); *Thelotrema erumpens* Magn., Arkiv Bot., Ser. 2, 3: 279 (1955). Lectotype (Hale 1978: 279). Hawaii, *Faurie 1909* (UPS!).

Thallus light grey-olive, smooth to uneven, with loose, irregular cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia immersed-erumpent, rounded, 0.4–0.7 mm diam.; disc covered by narrow, 0.05–0.1 mm wide pore; margin entire, brown-black. Columella absent. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, muriform, 35–50 × 15–20 µm, ellipsoid, with thick septa and diamond-shaped lumina (*Astrothelium*-like), colorless, I– (non-amyloid). Secondary chemistry: stictic and cryptostictic acids and (in variable amounts) peristictic, menegazziaic, constictic, and hypostictic acids.

Remarks:—This species externally resembles *Ocellularia pyrenuloides* Zahlbr. in the *Ocellularia* clade (Rivas Plata *et al.* 2012a, b), but the latter has a dense cortex and I+ violet-blue ascospores with lens-shaped lumina. Forms of *Clandestinotrema clandestinum* with indistinct columella differ by the dense cortex and smaller ascospores.

Specimens examined:—COSTA RICA. Cartago: Chiripó National Park, trail from Base Crestones to San Gerardo; 83° 29' W, 9° 29' N, 2500 m; disturbed primary mossy mountain forest, on trunk along trail; Mar 2000, *Sipman & Umaña 46569* (B, INB). Tapantí National Park, Macizo de la Muerte Section, Cerro de la Muerte (La Amistad Pacífico Conservation Area), Talamanca Ridge, km 93 on road (ruta 2) from Cartago to San Isidro, roadside; 83° 45' W, 9° 34' N, 3000–3100 m; upper montane cloud forest zone, disturbed low oak forest, on bark (lower trunk), semi-exposed; Jul 2002, *Sipman 48215b* (B, INB). San José: Cordillera de Talamanca, 5 km W of Cerro de la Muerte, San Gerardo de Dota, along Quebrada Ojo de Agua; 83° 48' W, 9° 35' N, 2600 m; epiphyte; Mar 1985, *Sipman & Chaverri 20795* (B, CR). San Gerardo de Dota, Finca Chacón, near entrance of Sendero La Quebrada; 83° 48' W, 9° 33' N, 2800 m, mixed, light, primary *Quercus* forest on steep slope, on think trunk; Nov 1999, *Sipman 44327* (B). San José: Cordillera de Talamanca, Interamerican Highway near El Empalme, S side of the highway to San Pablo; 9° 13' N, 83° 37' W, 2200 m; lower mountain rainforest; Dec 1978, *Kalb & Plöbst 38946* (hb. Kalb). San Gerardo de Dota, Finca Chacón, near entrance of Sendero La Quebrada; 83° 48' W, 9° 33' N, 2800 m; mixed, light, primary *Quercus* forest on steep slope; Nov 1999, *Sipman 44332* (B).

Clandestinotrema leucomelaenum **(Nyl.) Rivas Plata, Lücking & Lumbsch** (Fig. 12B)

Clandestinotrema leucomelaenum (Nyl.) Rivas Plata, Lücking & Lumbsch in Rivas Plata *et al.*, Fungal Diversity 52: 118 (2011); *Thelotrema leucomelaenum* Nyl., Acta Soc. Sci. Fenn. 7: 452 (1863); *Ocellularia leucomelaena* (Nyl.) Hale, Mycotaxon 11: 137 (1980). Lectotype (Hale 1974: 36). Colombia, *Lindig 2777* (H-NYL 22576!; isolectotypes: M!, UPS!).

Thelotrema leucomelaenum var. *elevatum* Vain., Ann. Acad. Sci. Fenn., Ser. A, 6(7): 137 (1915). Holotype. Lesser Antilles (Dominica), *Elliott 1534* (TUR-VAIN 26834!).

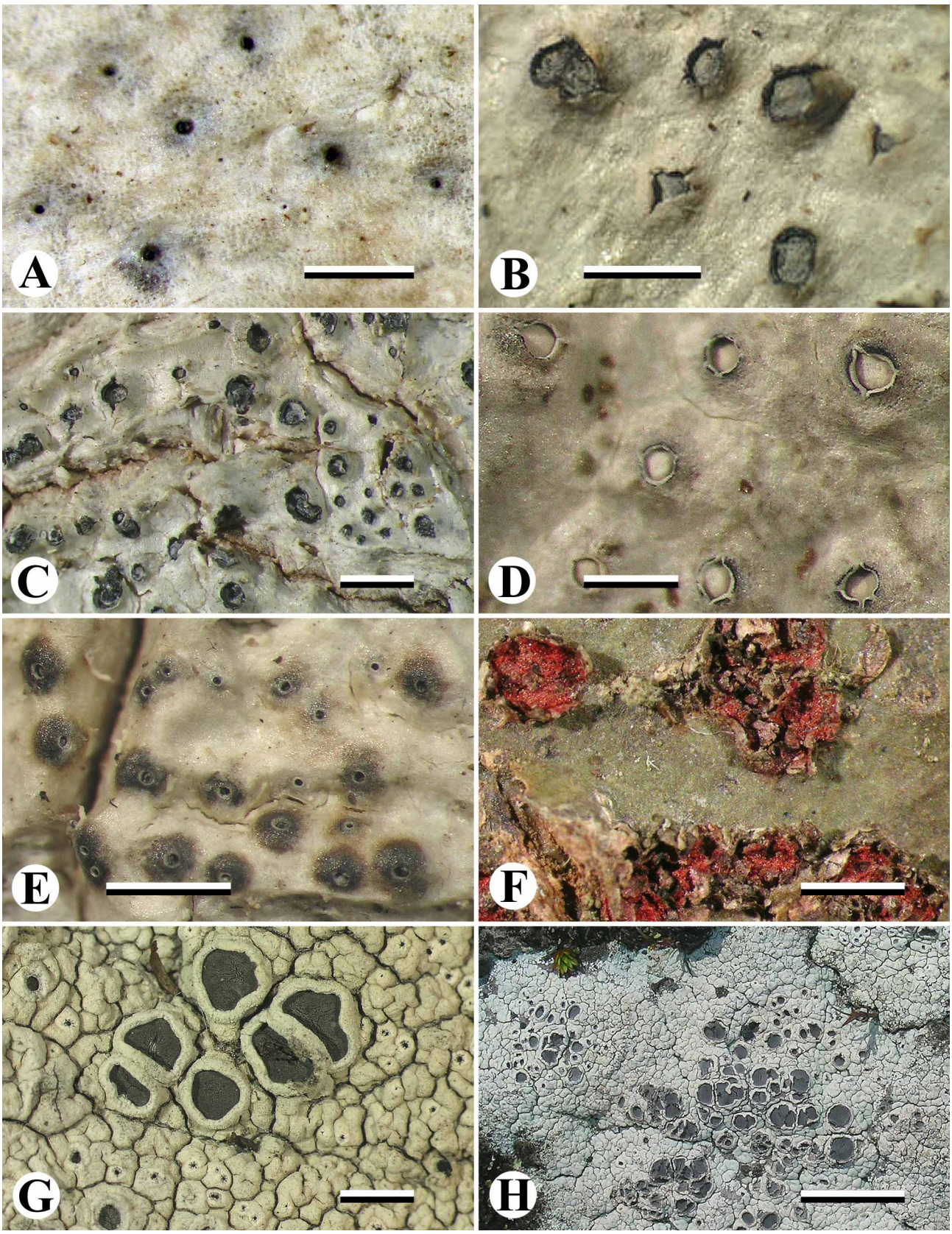

FIGURE 12. A. *Clandestinotrema erumpens*. B. *Clandestinotrema leucomelaenum*. C. *Clandestinotrema pauperius*. D. *Clandestinotrema stylothecium*. E. *Clandestinotrema tenue*. F. *Cruentotrema cruentatum*. G. *Diploschistes cinereocaesius*. H. *Diploschistes muscorum subsp. bartlettii*. Scale = 1 mm.

Thallus white-grey, smooth to uneven, ecorticate; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.4–0.8 mm diam.; disc partially covered by 0.2–0.4 mm wide pore which is filled by brown-black, white-pruinose columella; margin fissured, fused, brown-black. Columella present, broad-stump-shaped, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, muriform, 25–40 × 10–17 µm, ellipsoid, with thick septa and diamond-shaped lumina (*Astrothelium*-like), colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This forms part of a group of species that superficially resemble the genus *Melanotrema*, to the point that it seems difficult to believe that they are not congeneric. Yet, genetically the two lineages are very distinct and suggest a remarkable case of parallel evolution in the family (Rivas Plata & Lumbsch 2011a). Among the species of *Clandestinotrema* with *Melanotrema*-like thallus and apothecia, *C. leucomelaenum* is characterized by its comparatively large ascospores and lack of secondary substances. *Clandestinotrema cathomalizans* (see above) comes close but has stictic acid and an apically carbonized excipulum, whereas *C. pauperius* (see below) differs in the smaller, submuriform ascospores.

Specimens examined:—COSTA RICA. Alajuela: Between Volcán Poás and Volcán Barva, 3.5 km W of Carretera 9 turnoff; 84° 11' W, 10° 12' N, 2000 m; pasture with scattered trees; Jan 1979, *Hafellner s.n.* (B; Kalb, Lich. Neotrop. 433). La Palma de San Ramón; 1250 m; Oct 1929, *Brenes 106* (FH; as *Ocellularia excavata* var. *impressula* (Vain.) Zahlbr.). Volcán Tenorio National Park, Pilón Biological Station (Arenal-Tempisque Conservation Area), Tilarán Ridge, 140 km NW of San José, 25 km NNW of Tilarán, near Bijagua, main trail through forest to crater; 84° 59' W, 10° 43' N, 700–900 m; lower montane cloud forest zone, partly disturbed primary forest, on bark (lower trunk), semi-exposed; Mar 2004, *Lücking 17267e* (F, INB). Cartago: SW-slope of Volcán Turrialba, N of Santa Cruz, slope with forest relics N of Bonilla Arriba; 83° 42' W, 10° 01' N, 1500 m; epiphyte in forest; Mar 1985, *Sipman 20444* (B, CR). Puntarenas: Wilson Botanical Garden, Las Cruces Biological Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 190 km SE of San José, trail through botanical garden; 82° 58' W, 8° 47' N, 1200 m; montane rain forest zone, anthropogenic vegetation, on bark (lower trunk), semi-exposed; Sep 2007, *Lücking s.n.* (F). Puntarenas: La Amistad International Park, Altamira Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 20 km N of San Vito near Finca Colorado, interpretative trail (Sendero Gigantes) behind station; 83° 00' W, 9° 02' N, 1500–1600 m; montane rain forest zone, disturbed primary forest and secondary vegetation dominated by *Cecropia*, on bark (lower trunk) of *Cecropia*, semi-exposed; Jun 2002, *Sipman 48018h* (B, INB); ibid., on bark (lower trunk), partially shaded; Jun 2002, *Sipman 48032e* (B, INB); ibid., trail to Casa Coca; 83° 00' W, 9° 02' N, 1600–1800 m; montane rain forest zone, secondary forest and open secondary vegetation dominated by *Cecropia*, on bark (lower trunk), partially shaded; Jul 2002, *Sipman 48040a*, *48041* (B, INB); ibid., Cerro Biolley Section, Sabanas Esperanza (La Amistad Pacífico Conservation Area), Terraba Valley, 30 km NNW of San Vito near Biolley, lower trail from road to Sabanas Esperanza; 83° 03' W, 9° 04' N, 1300–1400 m; lowland to lower montane moist forest savanna zone, disturbed savanna vegetation with abundant shrubs and trees, on bark (lower trunk), exposed; Jul 2002, *Sipman 48111b* (B, INB). Las Tablas Protection Zone, Cedro Ridge, Las Alturas Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km NE of San Vito near Alturas, surroundings of station and trail into forest; 82° 50' W, 8° 57' N, 1600 m; montane rain forest zone, pasture with group of trees bordering forest, on bark (lower trunk), semi-exposed; Jun 2002, *Sipman 47818a* (B, INB). San José: Cordillera de Talamanca, Interamerican Highway near El Empalme, S side of the highway to San Pablo; 9° 13' N, 83° 37' W, 2200 m; lower mountain rainforest; Dec 1978, *Kalb & Plöbst 38928*, *38929*, *38931* (hb. Kalb).

Clandestinotrema pauperius **(Nyl.) Rivas Plata, Lücking & Lumbsch** (Fig. 12C)

Clandestinotrema pauperius (Nyl.) Rivas Plata, Lücking & Lumbsch in Rivas Plata *et al.*, Fungal Diversity 52: 118 (2011); *Thelotrema pauperius* Nyl., Ann. Sci. Nat. Bot., Sér. 5, 7: 318 (1867). Holotype. Colombia, *Lindig s.n.* (H-NYL 22607!; isotype: M!).

Thallus light yellow-grey, smooth to uneven, ecorticate; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.4–0.8 mm diam.; disc partially covered by 0.25–0.5 mm wide pore which is filled by brown-black, white-pruinose columella; margin fissured, brown-black. Columella present, broad-stump-shaped, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–1 longitudinal septa per segment, 15–25 × 6–8 µm, ellipsoid, with thick septa and diamond-shaped lumina (*Astrothelium*-like), colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Clandestinotrema pauperius* is the acid-deficient chemomorph of *C. stylothecium* (see below). As in other cases, we have kept these chemically different forms separate at the species level until molecular data proof the opposite. The holotype has mostly 3-septate ascospores (like those of *C. analorenae*), with some spores eventually becoming submuriform. It is thus set apart from *C. leucomelaenum* (see above), which is morphologically and chemically identical but has larger, muriform ascospores.

Specimens examined:—COSTA RICA. Alajuela: San Ramón Forest Reserve, near house at Río Lorencito, 5 km NE of Cerro Jabonal; 1000 m. 84° 37' W, 10° 13' N, 1000 m; humid, mossy forest with many ferns on mountain ridge, on canopy branches of fallen tree; Nov 1988, *Sipman et al. 41937* (B, CR). Puntarenas: Manuel Antonio National Park, near Quepos; 84° 09' W, 9° 23' N, sea level; scattered trees around hotel at end station of bus line; Nov 1988, *Sipman 42286* (B, CR). South of Las Cruces Botanical Garden, 5 km S of San Vito, Fila Cruces Ridge; 82° 57' W, 8° 43' N, 1200–1600 m; premontane forest zone; along road and at edge of cut forest; Dec 1978, *Wetmore 36931* (MIN).

Clandestinotrema stylothecium **(Vain.) Rivas Plata, Lücking & Lumbsch** (Fig. 12D)

Clandestinotrema stylothecium (Vain.) Rivas Plata, Lücking & Lumbsch in Rivas Plata *et al.*, Fungal Diversity 52: 118 (2011); *Thelotrema stylothecium* Vain., Étude Lich. Brésil 2: 80 (1890). Holotype. Brazil, *Vainio s.n.* (TUR-VAIN 26838!; isotypes: BM!, FH!, UPS!; Vainio, Lich. Bras. Exs. 1370).

Thallus light yellow-grey, smooth to uneven, ecorticate; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.4–0.8 mm diam.; disc partially covered by 0.25–0.5 mm wide pore which is filled by brown-black, white-pruinose columella; margin fissured, brown-black. Columella present, broad-stump-shaped, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–2 longitudinal septa per segment, 15–25 × 6–8 µm, ellipsoid, with thick septa and diamond-shaped lumina (*Astrothelium*-like), colorless, I– (non-amyloid). Secondary chemistry: stictic, constictic, cryptostictic, and hypostictic acids.

Remarks:—*Clandestinotrema stylothecium* and *C. leucomelaenum* (see above) are the two most commonly collected species in the genus and resemble each other closely, but the latter has larger ascospores and lacks secondary substances. The rare *Clandestinotrema pauperius* (see above) agrees in ascospore size and septation with *C. stylothecium* but also lacks secondary substances.

Specimens examined:—COSTA RICA. Cartago: Tapantí National Park, Tapantí Section, Tapantí Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 35 km SE of San José and 18 km SE of Cartago, trail above road (Sendero Árboles Caidos); 83° 47' W, 9° 45' N, 1400–1600 m; montane rain forest zone, closed primary forest and roadside, on bark (lower trunk), fully shaded; Apr 2003, *Lücking 16560* (F, INB). Guanacaste: Volcán Tenorio National Park, Alto Masis Section (Arenal-Tilarán Conservation Area), Tilarán Ridge, 125 km NW of San José, 15 km NNW of Tilarán, near Tierras Morenas, surroundings of station; 85° 00' W, 10° 37' N, 950–1000 m; lower montane elfin cloud forest zone, disturbed low elfin forest and secondary vegetation, on wood (fence post), exposed; Mar 2004, *Nelsen 3789* (INB, WIS); ibid., on bark (lower stem) of *Cecropia*, exposed; Mar 2004, *Will-Wolf 12784b* (INB, WIS); ibid., on bark (lower trunk),

exposed; Mar 2004, *Will-Wolf 12785b* (INB, WIS), *Lücking 17321b* (CR, F, INB, USJ, hb. Kalb); ibid., on bark (lower stem), exposed; Mar 2004, *Sipman 51917, 51925* (B, INB).

***Clandestinotrema tenue* (Hale) Rivas Plata, Lücking & Lumbsch** (Fig. 12E)

Clandestinotrema tenue (Hale) Rivas Plata, Lücking & Lumbsch in Rivas Plata *et al.*, Fungal Diversity 52: 118 (2011); *Thelotrema tenue* Hale, Smithson. Contr. Bot. 16: 38 (1974); *Ocellularia tenuis* (Hale) Hale, Mycotaxon 11: 138 (1980). Holotype. Lesser Antilles (Dominica), *Hale 35430* (US!).

Thallus white-grey, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.2–0.3 mm diam.; disc covered by narrow, 0.05–1 mm wide pore, filled by brown-black columella; margin entire, brown-black. Columella present, dark brown. Excipulum prosoplectenchymatous, dark brown; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–1 longitudinal septa per segment, 10–20 × 6–8 µm, ellipsoid, with thick septa and diamond-shaped lumina (*Astrothelium*-like), colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This species belongs in the group with narrow pore with entire margin and narrow columella. It resembles *Clandestinotrema clandestinum* (see above), but differs in the dark brown excipulum (not carbonized) and lack of secondary substances.

Specimens examined:—COSTA RICA. Alajuela: Volcán Tenorio National Park, Pilón Biological Station (Arenal-Tempisque Conservation Area), Tilarán Ridge, 140 km NW of San José, 25 km NNW of Tilarán, near Bijagua, main trail through forest to crater; 84° 59' W, 10° 43' N, 700–900 m; lower montane cloud forest zone, partly disturbed primary forest, on bark (twig), semi-exposed; Mar 2004, *Lücking 17262c* (F). Cartago: Genesis II Cloud Forest Reserve (La Amistad Pacífico Conservation Area), Talamanca Ridge, 2300–2400 m; upper montane rain forest zone, partly disturbed primary forest, on bark (lower trunk), semi-exposed; Feb 1997, *Lücking 97-39* (F). Río Macho Forest Reserve, La Esperanza del Guarco, 10 km S of El Empalme on road to San Isidro del General; 83° 55' W, 9° 41' N, 2500 m; primary *Quercus* forest on mountain ridge; Nov 1988, *Sipman et al. 41728* (B, CR). San José: Cordillera de Talamanca, Interamerican Highway near El Empalme, S side of the highway to San Pablo; 9° 13' N, 83° 37' W, 2200 m; lower mountain rainforest; Dec 1978, *Kalb & Plöbst 38930, 38938* (hb. Kalb). San Gerardo de Dota, Finca Chacón, near entrance of Sendero La Quebrada; 83° 48' W, 9° 33' N, 2800 m; mixed, light, primary *Quercus* forest on steep slope; Nov 1999, *Sipman 44316* (B).

***Cruentotrema* Rivas Plata, Papong, Lumbsch & Lücking**

Cruentotrema Rivas Plata, Papong, Lumbsch & Lücking in Rivas Plata *et al.*, Fungal Diversity 52: 119 (2011). Type. *Cruentotrema cruentatum* (Mont.) Rivas Plata, Lumbsch & Lücking.

Thallus olive-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer lacking clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded; disc hidden by a partially splitting thallus layer that exposes a deep red-pigmented medulla; margin formed by the outer portions of the thallus layer, lobulate to recurved, brown-black, red-pruinose. Columella absent. Excipulum prosoplectenchymatous, upper half carbonized in mature apothecia; periphysoids absent. Paraphyses unbranched. Ascospores 8/ascus, 3-septate to submuriform, ellipsoid, with thick septa and diamond-shaped lumina (*Astrothelium*-like), colorless, I– (non-amyloid). Secondary chemistry: no substances or medulla of apothecial margin in two species with dark red isohypocrellin.

Remarks:—This recently established genus is another segregate from *Ocellularia* s.lat. and, as *Clandestinotrema*, is closely related to *Dyplolabia* and *Fissurina* (Rivas Plata & Lumbsch 2011a; Rivas Plata *et al.* 2012a). In fact, *Cruentotrema* and *Dyplolabia*, although quite different morphologically, are hardly distinguishable genetically. The seemingly chroodiscoid apothecia somehow resemble those of *Chroodiscus*, *Chapsa*, and *Gyrotrema*, but their anatomy and ontogeny is very different. Whereas in the latter genera, the disc is exposed by the rupturing excipular and thalline margin, in *Cruentotrema* the thalline margin splits horizontally and only the outer part opens, whereas the inner part remains largely intact and covers the disc. The deep red pruina is thus not indicating the disc but the medulla of the splitting thalline margin. As in the case of the distantly related *Clandestinotrema* and *Melanotrema*, *Cruentotrema* finds a remarkable parallel taxon in the unrelated *Acanthothecis sanguinoloba* (Redinger) Staiger & Kalb, which has the same apothecial morphology and ontogeny but differs in its amyloid ascospores of the *Graphis* type and apically spinulose paraphyses (Staiger & Kalb 1999).

***Cruentotrema cruentatum* (Mont.) Rivas Plata, Lumbsch & Lücking** (Fig. 12F)

Cruentotrema cruentatum (Mont.) Rivas Plata, Lumbsch & Lücking in Rivas Plata *et al.*, Fungal Diversity 52: 119 (2011); *Stictis cruentata* Mont., Ann. Sci. Nat., Bot., Sér. 4, 3: 96 (1855). *Ocellularia cruentata* (Mont.) Hafellner & Magnes in Magnes, Biblioth. Mycol. 165: 119 (1997). Holotype. French Guiana, *Leprieur 805* (PC).

Arthothelium puniceum Müll. Arg., Hedwigia 32: 133 (1893); *Thelotrema puniceum* (Müll.Arg.) Makhija & Patw., Trop. Bryol. 10: 213 (1995); *Chapsa punicea* (Müll.Arg.) Cáceres & Lücking in Cáceres, Libri Bot. 22: 54 (2007). Holotype. Australia, *Bailey 369* (G!).

Thelotrema rhododiscum Homchantara & Coppins, Lichenologist 34: 135 (2002). Holotype. Thailand, *Homchantara 9676a* (RAMK!).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.6–1.2 mm diam.; disc hidden by a partially splitting thallus layer that exposes a deep red-pigmented medulla; margin formed by the outer portions of the thallus layer, lobulate to recurved, brown-black, red-pruinose. Columella absent. Excipulum prosoplectenchymatous, upper half carbonized; periphysoids absent. Hymenium 70–90 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 5–7 transverse septa and 0–1 longitudinal septa per segment, 20–30 × 10–12 µm, ellipsoid, with thick septa and diamond-shaped lumina (*Astrothelium*-like), colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC, medulla of apothecial margin with dark red isohypocrellin.

Remarks:—This rare but conspicuous species resembles a *Chapsa* or *Gyrotrema* but is set apart by the peculiar anatomy and ontogeny of the apothecia (see above) and the I-negative, *Astrothelium*-like ascospores. The thallus if often barely visible but the dark red apothecia characterize the species. *Cruentotrema cruentatum* is a lowland to montane rain forest species.

Specimens examined:—COSTA RICA. Guanacaste: Tropica Verde Reforestation Project (Tempisque Conservation Area), Nicoya Pensinsula, 150 km W of San José, 15 km SSE of Nicoya, near Hojancha, access road to site; 85° 23' W, 10° 01' N, 850–900 m; lowland to lower montane moist forest zone, exposed trees and fence posts along pasture, on bark (lower trunk), exposed; Mar 2004, *Sipman 52084* (B, INB). Puntarenas: Wilson Botanical Garden, Las Cruces Biological Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 190 km SE of San José, trail beyond botanical garden; 82° 58' W, 8° 47' N, 1200 m; montane rain forest zone, secondary forest, on bark (lower trunk), semi-exposed; Sep 2007, *Lücking 21006* (F).

Diploschistes Norman

Diploschistes Norman, Nyt. Mag. Naturvidensk. 7: 232 (1853). Type: *Diploschistes scruposus* (Schreb.) Norman.

Thallus saxicolous or terricolous or more rarely muscicolous, white-grey to yellow-grey, areolate-bullate, with loose cortex; medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded; disc exposed or covered by narrow pore, brown-black, white-pruinose; margin entire to fissured, with split between thallus and proper margin, brown-black, white-pruinose. Columella absent. Excipulum paraplectenchymatous, carbonized; periphysoids present, distinct. Paraphyses unbranched. Ascospores 4–8/ascus, submuriform to muriform, ellipsoid to fusiform, with slightly thickened septa and rectangular lumina, brown, I– (non-amyloid). Secondary chemistry: most species with lecanoric, gyrophoric, diploschistesic, and/or orcellinic acids.

Remarks:—*Diploschistes* is a rather unique genus due to its growth on mostly inorganic substrata. Anatomically, the genus somewhat resembles *Chapsa* and *Thelotrema* in the free, paraplectenchymatous excipulum with periphysoids, but is phylogenetically distinct (Staiger *et al.* 2006; Mangold *et al.* 2008a; Rivas Plata & Lumbsch 2011a, b). This correlates with the unique chemistry; diploschistesic and orcellinic acid are only found in this genus within the family and lecanoric and gyrophoric acid are otherwise extremely rare and only known from the unrelated genera *Dyplolabia* and *Ocellularia* (one species).

Key to the species of *Diploschistes* found in Costa Rica (4)

1. On rock; ascospores 4/ascus ..... ***D. scruposus***
- On soil or bryophytes (or juvenile parasitic on *Cladonia* lichens); ascospores 4–8/ascus 2

2. Thallus distinctly pruinose; apothecia often lobate ..... ***D. diacapsis***
- Thallus not or indistintly pruinose; apothecia angular-rounded 3

3. Thallus yellow-grey; ascospores 4–8/ascus; lecanoric, diploschistesic, and orcellinic acids ..... ***D. cinereocaesius***
- Thallus grey-green to pale blue-grey; ascospores 8/ascus; lecanoric and diploschistesic acids ..... ***D. muscorum* subsp. *bartlettii***

Diploschistes cinereocaesius (Sw.) Vain. (Fig. 12G)

Diploschistes cinereocaesius (Sw.) Vain., Ann. Acad. Sci. Fenn., Ser. A 15(6): 172 (1921); *Lichen cinereocaesius* Sw. in Acharius, Lichenogr. Suec. Prodrom.: 34 (1798); *Urceolaria cinereocaesia* (Sw.) Ach., Meth. Lich.: 148 (1803); *Lagerheimina cinereocaesia* (Sw.) Kuntze, Rev. Gen. Pl. 3: 478 (1891). Holotype. Lesser Antilles, s.col. (not seen).

Thallus yellow-grey, areolate-bullate, with loose cortex; medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 1–3 mm diam.; disc exposed, brown-black, white-pruinose; margin fissured, with split between thallus and proper margin, brown-black, white-pruinose. Columella absent. Excipulum paraplectenchymatous, carbonized; periphysoids present, distinct. Hymenium 100–120 µm high, clear; paraphyses unbranched. Ascospores 4–8/ascus, 18–31 × 9–15 µm, ellipsoid, with slightly thickened septa and rectangular lumina, brown, I– (non-amyloid), muriform. Secondary chemistry: lecanoric, diploschistesic, and orcellinic acids.

Remarks:—*Diploschistes cinereocaesius* is the most common species of the genus and the family in neotropical high montane areas. It is usually found on fine-grained soil between rocks. The species can be recognized by the characteristic yellowish color and the usually large apothecia. It is otherwise similar to *D. muscorum* subsp. *bartlettii* (see below).

Specimens examined:—COSTA RICA. Cartago: Volcán Irazú National Park (Cordillera Volcánica Central Conservation Area), Volcánica Central Ridge, 25 km ENE of San Jose, access road to summit craters and surroundings; 83° 51' W, 9° 59' N, 3300–3400 m; upper montane cloud forest and subalpine paramo zone, disturbed paramo vegetation and low roadside trees, on soil, fully exposed; Jul 2002, *Lücking 15540* (F, INB, USJ). San José: Los Santos Forest Reserve, Cerro de la Muerte (Pacífico Central Conservation Area), Talamanca Ridge, km 90 on road (ruta 2) from Cartago to San Isidro, access road to towers on summit; 83° 45' W, 9° 34' N, 3400–3500 m; upper montane cloud forest and subalpine paramo zone, disturbed low paramo shrub with Chusquea, on soil (humus), fully exposed; Sep 1987, *Lücking s.n.* (F); ibid., exposed; Jul 2002, Lücking 15341 (CR, F, INB, USJ); ibid., on rock, fully exposed; Jul 2002, *Lücking 15419b* (F, INB); ibid., on soil, fully exposed; Oct 2002, *Lizano et al. 29* (CR, INB, USJ); ibid., on soil, fully exposed; Nov 2002, *Lizano et al. 79* (USJ); ibid., on soil (humus), fully exposed; Apr 2003, *Buck 44213* (CRNY); ibid., on soil, fully exposed; Mar 2004, *Nelsen 3865* (INB, USJ, WIS); ibid., on rock (volcanic boulder), fully exposed; Mar 2004, *Aptroot 61053* (BR, INB).

***Diploschistes diacapsis* (Ach.) Lumbsch**

Diploschistes diacapsis (Ach.) Lumbsch, Lichenologist 20: 20 (1988); *Urceolaria diacapsis* Ach., Lich. Univ.: 339 (1810). Lectotype (Lumbsch 1988: 20). Spain, *Lagasca s.n.* (S!).

Thallus white-grey, areolate-bullate and heavily pruinose, with loose cortex; medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded to lobate, 1–4 mm diam.; disc exposed, brown-black to grey-black, thinly white-pruinose and often appearing bluish; margin entire to fissured, with split between thallus and proper margin, brown-black, white-pruinose. Columella absent. Excipulum paraplectenchymatous, carbonized; periphysoids present, distinct. Hymenium 110–180 µm high, clear; paraphyses unbranched. Ascospores 4–8/ascus, 20–40 × 9–17 µm, ellipsoid, with slightly thickened septa and rectangular lumina, brown, I– (non-amyloid), muriform. Secondary chemistry: lecanoric and diploschistesic acids.

Remarks:—*Diploschistes diacapsis* is another wide-spread and common species and is frequently found in the Neotropics. The species is often mistaken for *D. cinereocaesius* (which lacks a distinct thalline pruina and has a more yellowish thallus and contains additionally orcellinic acid) or *D. muscorum* subsp. *bartlettii* (which also lacks a distinct thallin pruina, overgrows lichens and bryophytes and has regularly 8-spored asci). *Diploschistes diacapsis* also seems to prefer more calcareous substrata (Lumbsch 1988, 1989).

Specimens examined:—COSTA RICA. Puntarenas: La Amistad International Park, Cerro Biolley Section, Sabanas Esperanza (La Amistad Pacífico Conservation Area), Terraba Valley, 30 km NNW of San Vito near Biolley, lower trail from road to Sabanas Esperanza; 83° 03' W, 9° 04' N, 1300–1400 m; lowland to lower montane moist forest savanna zone, disturbed savanna vegetation with abundant shrubs and trees, on soil, semi-exposed; Jul 2002, *Lücking 15310* (CR, F, INB, USJ).

***Diploschistes muscorum* subsp. *bartlettii* Lumbsch** (Fig. 12H)

Diploschistes muscorum subsp. *bartlettii* Lumbsch, Herzogia 7: 602 (1987). Holotype. New Zealand, *Bartlett 25905* (BM!).

Thallus light grey-green, pruinose, areolate-bullate, with loose cortex; medulla with clusters of calcium oxalate crystals. Apothecia immersed, angular-rounded, 1–2 mm diam.; disc exposed, brown-black, white-pruinose; margin entire, with split between thallus and proper margin, brown-black. Columella absent. Excipulum paraplectenchymatous, carbonized; periphysoids present, distinct. Hymenium 100–120 µm high,

clear; paraphyses unbranched. Ascospores 8/ascus, 18–32 × 6–15 µm, ellipsoid, with slightly thickened septa and rectangular lumina, brown, I– (non-amyloid), muriform. Secondary chemistry: lecanoric and diploschistesic acids.

Remarks:—This is a southern hemisphere taxon that can be found in tropical high montain areas, in particular on mossy road banks. It is easily confused with *Diploschistes cinereocaesius* (see above) but lacks a yellow tinge and the apothecia are smaller and sometimes lobate.

Specimens examined:—COSTA RICA. Alajuela: Volcán Tenorio National Park, Pilón Biological Station (Arenal-Tempisque Conservation Area), Tilarán Ridge, 140 km NW of San José, 25 km NNW of Tilarán, near Bijagua, access road to station and river; 84° 59' W, 10° 43' N, 700 m; lower montane cloud forest zone, exposed trees and fence posts along pasture, on rock (volcanic boulder), fully exposed; Mar 2004, *Aptroot 60425* (BR, INB). Cartago: Tapantí National Park, Macizo de la Muerte Section, Tres de Junio (La Amistad Pacífico Conservation Area), Talamanca Ridge, km 68 on road (ruta 2) from Cartago to San Isidro, roadside; 83° 51' W, 9° 40' N, 2700 m; upper montane cloud forest zone, disturbed upland peat bog with scattered shrubs and Blechnum, on debris (turf), semi-exposed; Mar 2004, *Aptroot 60987* (BR, INB). San José: Los Santos Forest Reserve, Cerro de la Muerte (Pacífico Central Conservation Area), Talamanca Ridge, km 90 on road (ruta 2) from Cartago to San Isidro, access road to towers on summit; 83° 45' W, 9° 34' N, 3400–3500 m; upper montane cloud forest and subalpine paramo zone, disturbed low paramo shrub with Chusquea, on rock (volcanic boulder), fully exposed; Mar 2004, *Aptroot 61047* (BR, INB).

***Diploschistes scruposus* (Schreb.) Norman** (Fig. 13A)

Diploschistes scruposus (Schreb.) Norman, Nytt Mag. Natur. 7: 232 (1853); *Lichen scruposus* Schreb., Spicil. Fl. Lipsiens.: 133 (1771); *Urceolaria scruposa* (Schreb.) Ach., Meth. Lich.: 147 (1803); *Parmelia scruposa* (Schreb.) Hepp, Flechtenfl. Würzb.: 43 (1824). Lectotype (Lumbsch 1989: 184). Germany, *von Schreber s.n.* (H-ACH 35!).

Thallus light grey-green, pruinose, areolate-bullate, with loose cortex; medulla with clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.7–1 mm diam.; disc exposed, black, white-pruinose; margin entire, without split between thallus and proper margin, brown-black, partially covered by thallus. Columella absent. Excipulum paraplectenchymatous, carbonized; periphysoids present, distinct. Hymenium 100–120 µm high, clear; paraphyses unbranched. Ascospores 4/ascus, 20–35 × 9–17 µm, muriform, ellipsoid, with slightly thickened septa and rectangular lumina, brown, I– (non-amyloid), muriform. Secondary chemistry: lecanoric and diploschistesic acids.

Remarks:—This is a cosmopolitan taxon that can occasionally be found in tropical high montain areas. It is easily confused with *Diploschistes cinereocaesius* (see above) but has smaller apothecia and grows over rock rather than soil.

Specimens examined:—COSTA RICA. San Jose: Cerro de la Muerte, along Panamerican Highway, 1 km N of Cerro Buenavista; 9° 33' N, 83° 46' W, 3400 m; 2 m tall scrub with rock outcrops, on rock; Mar 1985, *Sipman & Chaverri 20705* (B, CR).

Enigmotrema* Lücking, *gen. nov.

MycoBank #800224

Differing from *Cruentotrema* in the perithecioid ascomata with red pigment externally visible and unique apomorphies in the mtSSU sequence data which place the genus outside the *Cruentotrema-Dyplolabia* clade.

Type species:—*Enigmotrema rubrum* Lücking.

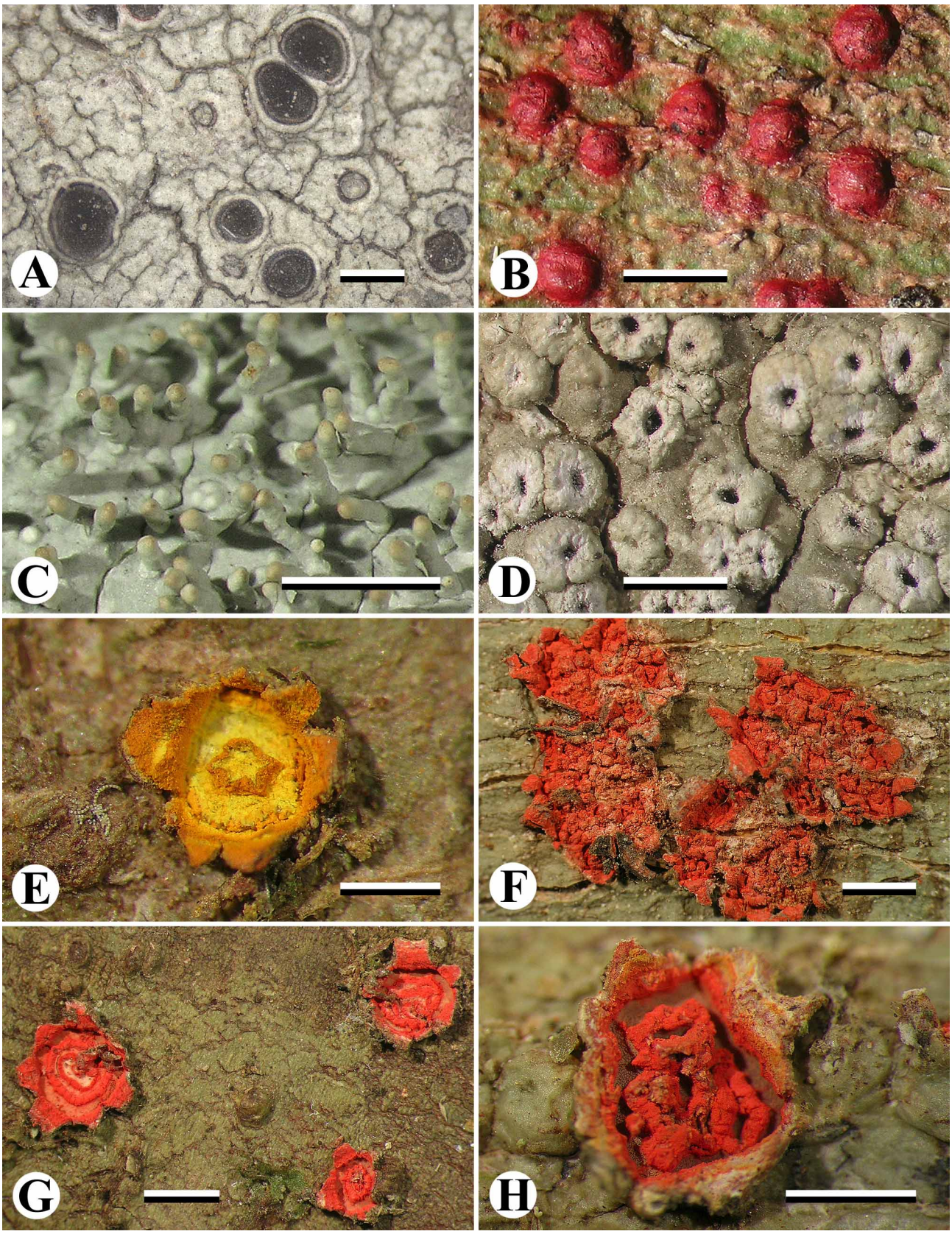

FIGURE 13. A. *Diploschistes scruposus*. B. *Enigmotrema rubrum*. C. *Fibrillithecis confusa*. D. *Fibrillithecis pachystoma*. E. *Gyrotrema aurantiacum*. F. *Gyrotrema papillatum*. G–H. *Gyrotrema wirthii*. Scale = 1 mm.

Thallus olive-green to olive-yellow, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer lacking clusters of calcium oxalate crystals. Apothecia erumpent to prominent, rounded, for a long time closed and appearing perithecioid, dark red, the cortex of the covering thallus layer first rupturing to expose the dark red medulla, the remaining thallus layer then rupturing into triangular teeth that remain involute, partially exposing the brown-black disc surface; margin remaining entire on the outside, forming a rim around the disc, dark red. Columella absent. Excipulum composed of large, thick-walled, rounded cells, for a long time uncarbonized but covering thallus lobes becoming apically carbonized in mature apothecia; periphysoids absent. Paraphyses unbranched. Ascospores (only few seen) presumably 8/ascus, 3-septate, ellipsoid, with thick septa and diamond-shaped lumina (*Astrothelium*-like), colorless, I– (non-amyloid). Secondary chemistry: no substances except medulla of apothecial margin with dark red isohypocrellin.

Remarks:—This new genus is here established on account of the unique apothecial development and mtSSU sequence data (Rivas Plata *et al.* 2012c). It is very similar to *Cruentotrema*, sharing several unique traits with the latter such as the thallus layer covering the apothecia rupturing to expose the red medulla. However, the ascoma development, with the apothecia remaining closed for a long time and closely resembling the perithecia of *Pyrenula cruentata*, is different from that of *Cruentotrema*. Genetically, *Enigmotrema* features unique apomorphies in the mtSSU gene partition and clusters outside *Cruentotrema*, but also within the *Fissurina* clade (Rivas Plata *et al.*, in prep.). Unfortunately, the type material has only premature and postmature apothecia; no asci and ascospores were found in the premature apothecia but ascospores were detected in the postmature apothecia which resemble those of *Clandestinotrema*, *Cruentotrema*, *Dyplolabia*, and some species of *Fissurina*, being consistent with the phylogenetic placement of this taxon in the *Fissurina* clade.

Enigmotrema rubrum* Lücking, *spec. nov. (Fig. 13B)
MycoBank #800225

Differing from *Cruentotrema* in the perithecioid ascomata with red pigment externally visible.

Holotype:—COSTA RICA. Puntarenas: Wilson Botanical Garden, Las Cruces Biological Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 190 km SE of San José, trail through botanical garden; 82° 58' W, 8° 47' N, 1200 m; montane rain forest zone, anthropogenic vegetation, on bark (lower trunk), semi-exposed; Sep 2007, *Lücking 21006* (F).

Thallus olive-green to olive-yellow, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer lacking clusters of calcium oxalate crystals. Apothecia erumpent to prominent, rounded, 0.7–1.2 mm diam., for a long time closed and appearing perithecioid, dark red, the cortex of the covering thallus layer first rupturing to expose the dark red medulla, the remaining thallus layer then rupturing into triangular teeth that remain involute, partially exposing the brown-black disc surface; margin remaining entire on the outside, forming a rim around the disc, dark red. Columella absent. Excipulum basally and laterally composed of large, thick-walled, rounded cells, for a long time uncarbonized but covering thallus lobes becoming apically carbonized in mature apothecia; periphysoids absent. Hymenium 50–60 µm high, clear; paraphyses unbranched. Ascospores (only few seen) presumably 8/ascus, 3-septate, 10–12 5–6 µm, ellipsoid, with thick septa and diamond-shaped lumina (*Astrothelium*-like), colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC, medulla of apothecial margin with dark red isohypocrellin.

Remarks:—This species was first mistaken for *Pyrenula cruenta* (Mont.) Vain., but microscopic analysis and molecular data revealed that it belonged in Graphidaceae. It shares several features with *Cruentotrema cruentatum* (see above) but differs in apothecial ontogeny and morphology and is also genetically different, clustering outside the *Cruentotrema-Dyplolabia* clade (Rivas Plata *et al.* 2012c).

Fibrillithecis Frisch

Fibrillithecis Frisch, Biblioth. Lichenol. 92: 135 (2006). Type. *Fibrillithecis vernicosa* (Zahlbr.) Frisch = *Fibrillithecis argentea* (Müll. Arg.) Rivas Plata & Lücking.

Thallus white-grey to light olive, smooth to uneven, sometimes producing isidia, with loose to dense cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent to sessile, rounded; disc covered by narrow pore, invisible. Margin fibrillate. Columella absent. Excipulum prosoplectenchymatous, colorless, apically above the hymenium projecting into parallel fibrils; periphysoids absent. Paraphyses unbranched. Ascospores 1–8/ascus, ellipsoid, with thick septa and rounded lumina, colorless, I+ violet-blue (amyloid), transversely septate to muriform. Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—*Fibrillithecis* is a recent segregate of of the collective genus *Myriotrema* (Frisch 2006). The excipular fibrils resemble the periphysoids found in *Thelotrema* and related genera, but differ in their apical position above (not lateral to) the hymenium; in addition, the excipulum is prosoplectenchymatous (myriotremoid) in *Fibrillithecis* and paraplectenchymatous in *Thelotrema* and allies (Frisch 2006; Rivas Plata *et al.* 2010a). The monophyly of *Fibrillithecis* and its close relationship with *Myriotrema* and *Ocellularia* and allies was shown in several molecular phylogenetic studies (Frisch *et al.* 2006; Mangold *et al.* 2008a; Rivas Plata & Lumbsch 2011a, b; Rivas Plata *et al.* 2012b).

Key to the species of *Fibrillithecis* found in Costa Rica (2)

1. Thallus with thick, erect isidia; ascospores submuriform, 14–23 × 8–12 µm ..... ***F. confusa***
- Thallus lacking isidia; ascospores 3-septate, 10–15 × 4–6 µm ..... ***F. pachystoma***

Fibrillithecis confusa Lücking, Kalb & Rivas Plata (Fig. 13C)

Fibrillithecis confusa Lücking, Kalb & Rivas Plata in Rivas Plata *et al.*, Lichenologist 42: 183 (2010). Holotype. Brazil, *Kalb 37602* (hb. Kalb).

Thallus light grey-olive to white-grey, smooth to uneven, producing isidia, with loose cortex; isidia 1–2 mm long and 0.15–0.25 mm thick, with rounded apex becoming brown with age; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent to sessile, rounded, 0.7–1.3 mm diam.; disc covered by narrow, 0.1–0.2 mm wide, fibrillate pore, not visible. Margin fibrillate, brown-black. Columella absent. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–2 longitudinal septa per segment, 14–23 × 8–12 µm, ellipsoid, with thick septa and rounded lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This species has a very similar relative in *Myriotrema hartii* (see below), a species that also has isidia, prominent to sessile apothecia, submuriform ascospores, and psoromic acid. The latter lacks fibrils, the isidia are decumbent, and the apothecia have a wider pore. When establishing *Fibrillithecis*, Frisch (2006) used the name *F. insignis* for the species with isidiate thallus, already noticing that the type of that species differed from the remaining material in certain aspects. Restudy of the type material showed that *Thelotrema insigne* is conspecific with *Myriotrema hartii* and a synonym of the latter, and thus a new name was required for the genuine *Fibrillithecis* with isidia, which was appropriately named *F. confusa* (Rivas Plata *et al.* 2010a). *Fibrillithecis confusa* can be considered the isidiate counterpart of *F. argentea*, an apparently palaeotropical species not yet found in Costa Rica (Rivas Plata *et al.* 2010a). The species is commonly found in semi-exposed situations in wet montane rain forest.

Specimens examined:—COSTA RICA. Cartago: Tapantí National Park, Macizo de la Muerte Section, La Esperanza Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, km 63 on road (ruta 2) from Cartago to San Isidro, access road to station; 83° 51' W, 9° 43' N, 2100–2200 m; montane cloud forest zone, partly disturbed oak forest, on bark (lower trunk), partially shaded; Jul 2002, *Lücking 15417* (F, INB); ibid., Tres de Junio (La Amistad Pacífico Conservation Area), Talamanca Ridge, km 70 on road (ruta 2) from Cartago to San Isidro, roadside; 83° 51' W, 9° 39' N, 2750 m; upper montane rain forest zone, open upland peat bog with *Blechnum* and *Puya*, on rock (boulder), fully exposed; Jul 2002, *Lücking 15438e* (CR, F, INB). Guanacaste: Volcán Tenorio National Park, Alto Masis Section (Arenal-Tilarán Conservation Area), Tilarán Ridge, 125 km NW of San José, 15 km NNW of Tilarán, near Tierras Morenas, surroundings of station; 85° 00' W, 10° 37' N, 950–1000 m; lower montane elfin cloud forest zone, disturbed low elfin forest and secondary vegetation, on bark (lower stem), semi-exposed; Mar 2004, *Will-Wolf 12781* (F, INB, WIS); ibid., on bark (branch), exposed; Mar 2004, *Lücking 17322* (CR, F, INB, USJ). San José: Braulio Carrillo National Park, 1 km before tunnel; Sep 1986, *Campos 80* (B).

Fibrillithecis pachystoma* (Nyl.) Sipman, *comb. nov. (Fig. 13D)
MycoBank #800067

Thelotrema pachystomum Nyl., Ann. Sci. Nat. Bot., Ser. 4, 11: 221 (1859) [non *Thelotrema pachystomum* Leight. = *Ocellularia massalongoi* (Mont.) Hale]; *Myriotrema pachystomum* (Nyl.) Hale, Mycotaxon 11: 134 (1980). Lectotype (Hale 1978: 26). Peru, *Weddell s.n.* (PC!).

Thallus light grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.7–1.4 mm diam.; disc covered by narrow, 0.1–0.2 mm wide, fibrillate pore, invisible. Margin fibrillate, brown-black. Columella absent. Excipulum prosoplectenchymatous, apically dark brown; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3-septate, 10–15 × 4–6 µm, ellipsoid, with thick septa and rounded lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This species is set apart from the other species of the genus by the 3-septate ascospores. It otherwise closely resembles *F. argentea* (Rivas Plata *et al.* 2010a).

Specimens examined:—Not yet found in Costa Rica but reported from Panama (Hale 1978).

Gyrotrema Frisch

Gyrotrema Frisch in Frisch & Kalb, Biblioth. Lichenol. 92: 379 (2006). Type. *Gyrotrema sinuosum* (Sipman) Frisch.

Thallus grey-green to olive-green, smooth to uneven, rarely papillose, with dense, prosoplectenchymatous cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent, rounded; disc exposed, orange-yellow to cinnabar-red or pink, rarely white; margin lobulate to recurved, fused, pigmented inside in species with pigmented disc. Columella absent but concentric rings of excipular tissue separating rings of old hymenia, with youngest hymenium ring next to margin. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Paraphyses unbranched. Ascospores 8/ascus, transversely septate, ellipsoid to oblong, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances or hypoprotocetraric acid, apothecial disc with anthraquinones.

Remarks:—*Gyrotrema* is one of the most conspicuous genera in the thelotremoid Graphidaceae, due to its large and showy apothecia. The apothecia at first glance resemble those of *Chroodiscus* but have a fundamentally different anatomy. The concentric rings of regenerated hymenia, separated by concentrically

arranged old excipular tissue, are a unique feature in the family (Frisch & Kalb 2006), but remotely comparable to the striation in *Graphis* and similar genera (Staiger 2002). *Gyrotrema* appears to have a pronounced seasonality in hymenium and ascospore production, which could explain why ascospores are very difficult to find. Fortunately, the ascospores are quite similar in the species known to date and not necessary for species identification, which is rather done by chemistry and apothecial pigmentation. Molecular phylogeny places *Gyrotrema* close to *Ocellularia* s.str., i.e. *O. cavata* and allies (Rivas Plata *et al.* 2012b). The latter species frequently have a pigmented medulla in the apothecial margins and a tendency towards marginal striation can be found in *O. crocea* (Kremp.) Overeem & D. Overeem (Hale 1978). Yet, morphologically *Gyrotrema* is quite distinctive when compared to *O. cavata* and relatives. The species of *Gyrotrema* are typical elements of corticolous lowland rain forest lichen communities in the shady understory.

Key to the species of *Gyrotrema* found in Costa Rica (3)

1. Apothecial disc yellow-orange, K+ dark red ..... ***G. aurantiacum***
- Apothecial cinnabar-red, K+ purple 2

2. Apothecia 1–5 mm diam., irregularly lobate; thallus with numerous white papillae ..... ***G. papillatum***
- Apothecia 0.5–2 mm diam., angular-rounded; thallus lacking white papillae ..... ***G. wirthii***

Gyrotrema aurantiacum* Sipman, Lücking & Chaves, *spec. nov. (Fig. 13E)
MycoBank #800076

Differing from *Gyrotrema* wirthii in the yellow-orange apothecial disc.

Holotype:—COSTA RICA. Puntarenas: Carara National Park, Quebrada Bonita Section (Pacífico Central Conservation Area), 60 km WSW of San Jose on road from Orotina to Quepos (34), trail from visitor's center to Quebrada Bonita; 84° 35' W, 9° 47' N, 100 m; lowland moist forest zone, partly disturbed dense primary forest with understory dominated by *Erythrochiton gymnanthus*, on bark (lower trunk), partially shaded; Jul 2002, *Sipman 48393* (INB-0003987224; isotypes: F, B).

Thallus olive-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 1–3 mm diam.; disc exposed, orange-yellow; margin lobulate to recurved, fused, orange inside. Columella absent but concentric rings of excipular tissue separating rings of old hymenia, with youngest hymenium ring next to margin. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores possibly 8/ascus, 7-septate, 20–30 × 5–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC, apothecial disc with yellow-orange (K+ dark red) anthraquinone.

Remarks:—This species is described formally even though only two ascospores were found in the entire, otherwise well-devoped and rich material. Ascospores are similar to those of *G. wirthii* (see below) but the apothecial pigment in *G. aurantiacum* is different, being yellow above the hymenial rings and orange above the concentric excipular remnants. Since species of *Gyrotrema* differ principally in their chemistry and apothecial pigmentation (Frisch 2006; Rivas Plata *et al.* 2008b), we consider this a species-level difference. This is confirmed by a geographic differentiation: whereas the type species, *G. sinuosum*, with pink apothecia, is known from Amazonia, the cinnabar-red *G. wirthii* has only been found in the southern Pacific lowlands of Costa Rica and the yellow-orange *G. aurantiacum* in the central Pacific region of that country.

***Gyrotrema papillatum* Lücking** (Fig. 13F)

Gyrotrema papillatum Lücking in Lumbsch *et al.*, Phytotaxa 18: 63 (2011). Holotype. Costa Rica, *Lücking 16301* (F!; isotype: INB!).

Thallus grey-green to olive-green, with numerous white papillae, with dense, prosoplectenchymatous cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent, rounded to lobate, 1–5 mm diam.; disc exposed, cinnabar-red; margin lobulate to recurved, fused, cinnabar-red inside. Columella absent but concentric rings of excipular tissue separating rings of old hymenia, with youngest hymenium ring next to margin. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–9-septate, 25–30 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC, apothecial disc with cinnabar-red (K+ purple) anthraquinone.

Remarks:—*Gyrotrema papillatum* closely resembles *G. wirthii* (see below) and has the same apothecial pigment. However, its apothecia are larger and more irregular and its thallus is densely white-papillose. The papillae are formed by colorless tissue of fungal hyphae and do not appear to be pycnidia; no conidia or conidigeneous tissue was found in microscopic sections. Whereas *G. wirthii* has been found in the southern part of the Osa Pensinsula, *G. papillatum* is known from a rich collection from the central part close to the Golfo Dulce coast. It thus seems that also in this case, a microgrographic differentiation supports the separation of these two species. Both the type of *G. wirthii* and that of *G. papillatum* have been sequenced and the mtSSU sequences are very similar (Rivas Plata *et al.* 2012b); however, in both cases only a short fragment was obtained and the more variable parts of the mtSSU that would indicate specific differences are lacking.

***Gyrotrema wirthii* Rivas Plata, Lücking & Lumbsch** (Fig. 13G–H)

Gyrotrema wirthii Rivas Plata, Lücking & Lumbsch in Rivas Plata *et al.*, Sauteria 15: 418 (2008). Holotype: Costa Rica, *Lücking 16252b* (INB-4003214!; CR!, F!, US!, isotypes).

Thallus grey-green to olive-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 1–3 mm diam.; disc exposed, cinnabar-red; margin lobulate to recurved, fused, cinnabar-red inside. Columella absent but concentric rings of excipular tissue separating rings of old hymenia, with youngest hymenium ring next to margin. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–7-septate, 20–28 × 5–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC, apothecial disc with cinnabar-red (K+ purple) anthraquinone.

Remarks:—This is the most common species of the genus in Costa Rica and especially abundant in the southern Pacific lowlands of the Osa Peninsula (Rivas Plata *et al.* 2008b).

Specimens examined:—COSTA RICA. Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, round trail NW of station (Sendero Sirena and Sendero Guanacaste); 83° 35' W, 8° 29' N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (lower stem), partially shaded; Apr 2003, *Lücking 16241* (F), *16252b* (CR, F, INB, USJ), *Sipman 51162a* (B, INB); ibid., second part of trail from Los Patos to Sirena station; 83° 33' W, 8° 32' N, sea level; lowland rain forest zone, oldgrowth secondary forest and closed secondary vegetation, on bark (lower stem), semi-exposed; Apr 2003, *Sipman 51105a* (B, CR). Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), partially shaded; Feb 1997, *Lücking 97-116* (F), *97-123* (CR), *97-172* (F).

Leptotrema Mont. & v. d. Bosch

Leptotrema Mont. & v. d. Bosch in Miquel, Plantae Junghuhnianae Fasc. IV: 483 (1855); Frisch, Biblioth. Lichenol. 92: 142 (2006). Type. *Leptotrema wightii* (Tayl.) Müll. Arg.

Thallus light grey-olive, smooth to uneven, distinctly gall-forming, with loose cortex; photobiont layer and medulla with columnar clusters of calcium oxalate crystals and sometimes with scattered clusters of blood-red crystals. Apothecia immersed, rounded; disc covered by narrow pore, invisible; margin entire, with (indistinct) split between thallus and proper margin, grey-brown. Columella absent. Excipulum paraplectenchymatous, pale brown; periphysoids absent. Paraphyses unbranched but laterally anastomosing. Ascospores 8/ascus, submuriform, ellipsoid, with thick septa and rounded lumina, brown, young I+ violet-blue (amyloid), submuriform. Secondary chemistry: no substances or hypoprotocetraric acid, medulla with crystal clusters of red anthraquinone in the type species.

Remarks:—*Leptotrema* was resurrected by Frisch (2006) for the single species, *L. wightii*, which is a peculiar taxon recognized by its gall-forming thallus, myriotremoid apothecia, and red crystal clusters in the medulla. *Leptotrema wightii* resembles species in *Leucodecton*, such as *L. glaucescens* and *L. phaeosporum* (Nyl.) Rivas Plata & Lücking, both morphologically and anatomically, but is genetically quite distinct and clusters with the enigmatic *Reimnitzia santensis* (Rivas Plata & Lumbsch 2011a, b; Rivas Plata *et al.* 2012b). Non-molecular support for this relationship is found in the thallus structure, ascospore type, and the somewhat odd asci in both genera (Frisch 2006).

Leptotrema wightii (Tayl.) Müll. Arg (Fig. 14A–B)

Endocarpon wightii Tayl. in Hook., London J. Bot. 6: 155 (1847); *Thelotrema wightii* (Tayl.) Nyl., Mém. Soc. Sci. Cherbourg 5: 118 (1857); *Leptotrema wightii* (Tayl.) Müll. Arg., Flora 65: 499 (1882); *Phaeotrema wightii* (Tayl.) Zahlbr., Ark. Bot. 31A(1): 48 (1944); *Myriotrema wightii* (Tayl.) Hale, Mycotaxon 11: 135 (1980). Lectotype (Hale 1974: 43). India, *Wight 89* (FH!isolectotypes: BM!, G!).

Leptotrema prevostianum Mont., Ann. Sci. Nat. Bot., Sér. 3, 16: 292 (1849); *Leptotrema prevostianum* (Mont.) Mont., Syll. Gen.: 364 (1856). Lectotype (Hale 1974: 43). Antilles, *Prévost s.n.* (PC!).

Thelotrema ravenelii Tuck., Amer. J. Arts Sci, Ser. 2, 25: 426 (1858); *Leptotrema ravenelii* (Tuck.) Fink, Lichen Fl. United States: 133 (1935). Lectotype (Salisbury, 1971: 35). U.S.A., *Ravenel 151* (FH!; isolectotypes: NY!, US!).

Thelotrema subconcretum Leight., Trans. Linn. Soc. London 27: 169 (1869); *Phaeotrema subconcretum*(Leight.) Müll. Arg., Mém. Soc. Phys. Genève 29(8): 10 (1887); *Leptotrema subconcretum* (Leight.) Müll. Arg., Nuovo Giorn. Bot. Ital. 23: 277 (1891). Lectotype (Hale 1974: 43). Sri Lanka, *Thwaites 89* (BM!).

Leptotrema foraminulosum Kremp., Nuovo Giorn. Bot. Ital. 7: 20 (1875); *Phaeotrema foraminulosum* (Kremp.) Zahlbr., Cat. Lich. Univ. 2: 607 (1923). Holotype. Malaysia (Borneo), *Beccari 112* (M!; isotype: G!).

Endocarpon baileyi Stirt., Trans. Proc. Roy. Soc. Victoria 17: 74 (1881); *Leptotrema baileyi* (Stirt.) Shirley, Proc. Roy. Soc. Queensland 6: 194 (1889). Holotype. Australia, *Bailey 249* (GLAM!; isotype: BRI!).

Leptotrema flavicans Müll. Arg., Rev. Mycol. 10: 114 (1888). Holotype. Paraguay, *Balansa 4170* (G!; isotypes: BM!, M!).

Leptotrema wightii var. *saxicola* Redinger, Arkiv Bot. 28A: 113 (1936). Holotype. Brazil, *Malme 3788* (S!).

Thallus light grey-olive, gall-forming but otherwise smooth, with loose cortex; photobiont layer and medulla with columnar clusters of calcium oxalate crystals and medulla with scattered clusters of blood-red crystals. Apothecia immersed, rounded, 0.1–0.3 mm diam.; disc covered by narrow, 0.05–0.2 mm wide pore, invisible; margin entire, with (indistinct) split between thallus and proper margin, grey-brown. Columella absent. Excipulum paraplectenchymatous, pale brown; periphysoids absent. Hymenium 100–150 µm high, clear; paraphyses unbranched but laterally towards the excipulum anastomosing. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–2 longitudinal septa per segment, 20–30 × 9–13 µm, ellipsoid, with thick septa and rounded lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC, medulla with crystal clusters of bright red anthraquinone.

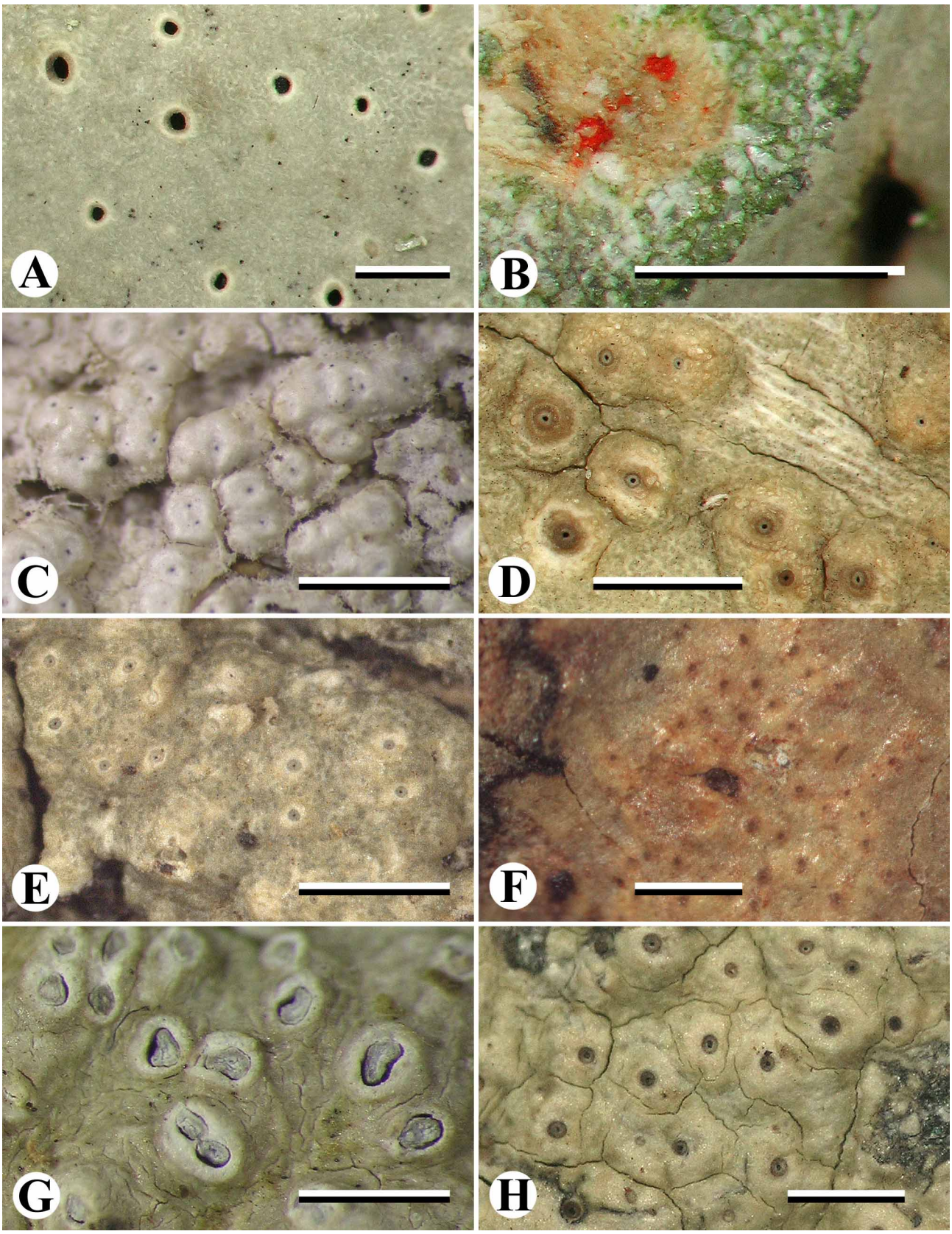

FIGURE 14. A–B. *Leptotrema wightii*. C. *Leucodecton album*. D. *Leucodecton bisporum*. E. *Leucodecton compunctellum*. F. *Leucodecton compunctum*. G. *Leucodecton expallescens*. H. *Leucodecton fissurinum*. Scale = 1 mm.

Remarks:—*Leptotrema wightii* is a very characteristic species, easily recognized by the gall-forming thallus with columnar clusters of calcium oxalate crystals and with red crystal clusters interspersed in the medulla, in combination with myriotremoid apothecia producing submuriform, brown ascospores. The gall-forming thallus, which is hollow underneath, with the cavity usually colonized by ants, is a rare feature within the family but found in unrelated species in several genera, such as *Leucodecton*, *Ocellularia*, and *Thelotrema* (Rivas Plata & Lumbsch 2011). Most similar in thallus structure and anatomy as well as ascospore type is the closely related *Reimnitzia santensis* (see below), but that species has large, chroodiscoid apothecia and produces isidia; it also lacks red crystal clusters in the thallus. *Thelotrema leiospodium* Nyl., described from Portugal and growing over soil, was synonymized with *L. wightii* by Frisch (2006); however, the type material shows a deviating thallus anatomy lacking columnar and red crystals, as well as larger apothecia with free excipulum, and has been accepted as species in *Thelotrema* (Mangold *et al.* 2009; Rivas Plata *et al.* 2010a). There are also great similarities with *Leucodecton desquamescens* (Vain.) Rivas Plata & Lücking (Rivas Plata *et al.* 2010a), which differs in the much larger apothecia with exposed disc and the lack of red crystals in the medulla. *Leptotrema wightii* is commonly found on shaded to semi-exposed tree trunks in rain forest and semi-deciduous dry forest.

Specimens examined:—COSTA RICA. Guanacaste: Lomas de Barbudal Biological Reserve, Lomas de Barbudal Station (Tempisque Conservation Area), Río Tempisque Bassin, 140 km WNW of San José and 20 km WSW of Bagaces, trail from station to Río Barbudal; 85° 22' W, 10° 30' N, 100 m; lowland to lower montane moist forest zone, disturbed gallery forest and forest remnants, on bark (lower trunk), semi-exposed; Mar 2003, *Nelsen 3534* (INB, WIS); ibid., on bark (lower trunk) of Ficus, partially shaded; Mar 2003, *Lücking 16117b* (F, INB,). Puntarenas: Las Tablas Protection Zone, La Neblina Section (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km ENE of San Vito near Las Mellizas, access road to fincas; 82° 45' W, 8° 55' N, 1600 m; montane rain forest zone, disturbed primary forest and pasture, on wood (log, rotten), fully shaded; Jun 2002, *Nelsen 2034a* (F, INB, hb. Nelsen); ibid., Los Portones Section (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km ENE of San Vito, 5 km on gravel road from Progreso to Las Tablas, roadside; 82° 48' W, 8° 55' N, 1600 m; montane rain forest zone, secondary forest and disturbed remnants of primary forest, on bark (lower trunk), partially shaded; Jun 2002, *Will-Wolf 10043a* (F, INB, WIS).

Leucodecton A. Massal.

Leucodecton A. Massal., Atti Reale Ist. Veneto Sci. Lett. Arti, Ser. 3(5): 325 (1860). Type. *Leucodecton compunctum* (Ach.) A. Massal.

Thallus variously colored, smooth to uneven or minutely grainy, sometimes gall-forming, ecorticate or with loose (rarely dense) cortex; photobiont layer and medulla with (often columnar) clusters of calcium oxalate crystals. Apothecia immersed to erumpent, rounded; disc usually covered by narrow pore, rarely partially exposed; margin entire to minutely lobulate, usually with split between thallus and proper margin (double margin), variously colored. Columella absent. Excipulum paraplectenchymatous, colorless to brown; periphysoids absent. Paraphyses unbranched. Ascospores 1–8/ascus, transversely septate to muriform, ellipsoid to oblong, with slightly thickened septa and rounded lumina, colorless to mostly brown, I– or young slightly I+ violet-blue (amyloid). Secondary chemistry: no substances or mostly stictic acid and satellites, rarely norstictic acid.

Remarks:—*Leucodecton* is an enigmatic genus as most species resemble the genus *Leptotrema* in many aspects, such as thallus morphology, apothecial type, excipulum structure, and ascospores (Frisch 2006). However, the two genera are not closely related: while *Leptotrema* and *Reimnitzia* form a clade sister to the *Ocellularia* clade, *Leucodecton* is well supported within the *Chapsa-Thelotrema* clade (Mangold *et al.* 2008a; Papong *et al.* 2009a; Rivas Plata & Lumbsch 2011a, b). This is surprising as it is the only lineage within this

clade lacking periphysoids. On the other hand, the secondary chemistry of *Leucodecton* is well in line with *Chapsa* and *Thelotrema*, with stictic acid being the dominant component, and all three genera share the paraplectenchymatous excipulum and the often thick outer ascospore walls. Two species of *Leucodecton*, *L. glaucescens* and *L. occultum*, do resemble a minute *Chapsa* and *Thelotrema*, respectively, and both are phylogenetically at the base of the *Leucodecton* clade, suggesting that the *Leptotrema*-type morphology of other species, such as *Leucodecton phaeosporum* (Nyl.) Rivas Plata & Lücking (Rivas Plata *et al.* 2010a), is derived and evolved parallel to that of *Leptotrema* (Rivas Plata & Lumbsch 2011a).

Key to the species of *Leucodecton* found or expected in Costa Rica (10)

1. Thallus with coarse isidioid outgrowths; ascospores transversely septate ..... ***L. dactyliferum***
- Thallus lacking isidioid outgrowths; ascospores (sub-)muriform 2

2. Ascospores 60–180 µm long, 1–4 per ascus 3
- Ascospores 10–40 µm long, (2–)4–8 per ascus 4

3. Hymenium inspersed; ascospores up to 180 × 40 µm ..... ***L. bisporum***
- Hymenium clear; ascospores usually less than 100 µm long, rarely up to 140 µm in single-spored asci ..... ***L. compunctellum***

4. No substances; apothecia porinoid, with pore almost invisible; thallus with dense, shiny cortex ..... ***L. compunctum***
- Norstictic or stictic acid; apothecia variable 5

5. Norstictic acid; apothecia minutely lepadinoid, with free excipulum and double margin ..... ***L. occultum***
- Stictic acid; apothecia distinctly lepadinoid, chroodiscoid, myriotremoid or porinoid 6

6. Ascospores persistently colorless; apothecia distinctly lepadinoid ..... ***L. expallescens***
- Ascospores becoming brown; apothecia chroodiscoid, myriotremoid or porinoid 7

7. Thallus gall-forming; apothecia usually aggregate and often forming whitish pseudostromata, minutely chroodiscoid; ascospores less than 20 × 10 µm ..... ***L. glaucescens***
- Thallus not gall-forming; apothecia solitary (although sometimes numerous), myriotremoid or porinoid; ascospores usually larger than 20 × 10 µm and up to 35 × 18 µm 8

8. Thallus grainy with columnar clusters of crystals and loose cortex ..... ***L. sordidescens***
- Thallus smooth (but sometimes fissured) with irregular crystals and dense cortex 9

9. Apothecia 0.2–0.3 mm diam., prominent; thallus and apothecia whitish ..... ***L. album***
- Apothecia 0.4–0.8 mm diam., erumpent; thallus and apothecia light grey-olive ..... ***L. fissurinum***

Leucodecton album* Lücking & Sipman, *spec. nov. (Fig. 14C)
MycoBank #800077

Differing from *Leucodecton fissurinum* in the smaller, more prominent apothecia and white thallus.

Holotype:—COSTA RICA. San José: San Gerardo de Dota, Finca Chacón, near entrance of Sendero La Quebrada; 9° 33' N, 83° 48' W, 2800 m; mixed, light, primary *Quercus* forest on steep slope, on sapling; Nov 1999, *Sipman 44336* (B).

Thallus white, smooth, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with irregular (not columnar) clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.2–0.3 mm diam.; disc concealed by minute, ostiolate, 0.03–0.05 mm wide pore, invisible; margin entire, white. Columella absent. Excipulum paraplectenchymatous, brown; periphysoids absent. Hymenium 140–180 µm

high, clear; paraphyses unbranched. Ascospores 8/ascus, muriform, 25–32 × 14–16 µm, ellipsoid, with thickened septa and rounded lumina, pale grey-brown to brown when old, young I+ pale violet-blue (amyloid). Secondary chemistry: stictic, hypostictic, cryptostictic, and constictic acids (surface UV–; medulla C–, P+ orange; section with K+ persistently yellow efflux).

Remarks:—This new species is known from a single collection only but is described here formally since its characteristic morphology does not fit any other species of the genus. The whitish thallus and prominent apothecia with narrow pore are reminescent of *Fibrillithecis*, but the internal anatomy and the chemistry place this species in *Leucodecton*. Morphologically and chemically most similar is *L. fissurinum* (see below), which has larger, erumpent apothecia with wider pore.

Leucodecton bisporum* (Nyl.) Sipman & Lücking, *comb. nov. (Fig. 14D)
MycoBank #800064

Thelotrema bisporum Nyl., Mém. Soc. Sci. Nat. Cherbourg 5: 118 (1857); Nylander in Hue, Nouv. Arch. Mús., Sér. 3, 3: 96 (1891). *Leptotrema bisporum* (Nyl.) Riddle in Britton & Millspaugh, Bahama Fl.: 545 (1920) [non *Leptotrema bisporum* Szatala, nom. illeg.]. Holotype. Lesser Antilles (Guadeloupe), *L'Herminier s.n.* (H-NYL 22489!).

Thallus light grey-olive-yellow, with minutely grainy surface, with loose cortex; photobiont layer and medulla with columnar clusters of calcium oxalate crystals. Apothecia immersed to erumpent, rounded, 0.3–0.5 mm diam.; disc concealed by minute, ostiolate, 0.03–0.05 mm wide pore, invisible; margin entire, brown, forming brown spot around ostiole. Columella absent. Excipulum paraplectenchymatous, pale brown; periphysoids absent. Hymenium 150–200 µm high, inspersed; paraphyses unbranched. Ascospores 1–4/ascus, richly muriform, 90–180 × 20–40 µm, richly muriform, oblong, with slightly thickened septa and rectangular lumina, brown, I– (non-amyloid) or weakly I+ violet-blue (amyloid) when young. Secondary chemistry: stictic, constictic, hypoconstictic and cryptostictic acids.

Remarks:—This material was first identified as *Myriotrema reclusum*, which is now considered a synonym of *Leucodecton compunctellum* (Mangold *et al.* 2009; see below). The latter agrees with *L. bisporum* in all aspects except that the hymenium is not inspersed. Most Costa Rican specimens have an inspersed hymenium and must be identified with *L. bisporum*. Both species have the disc completely concealed by a very narrow, ostiolate pore and are thus easily mistaken for pyrenocarpous lichens, particularly *Pyrenula*, because of the brown ascospores. Contrary to most other thelotremoid Graphidaceae, the two species prefer more exposed microsites, such as the bark of *Cococ nucifera*, a substrate they principally share with pyrenocarpous taxa. All collections cited below are from coastal rain forest. This species should not be confused with *Leptotrema bisporum* Szatala which is a synonym of *Thelotrema lepadodes* (see below).

Specimens examined:—COSTA RICA. Limón: Caribbean coast, S of Cahuita; 82° 50' W, 9° 44' N, sea level; *Cocos* trunks in orchard immediately S of the town; Jan 1979, *Sipman 12245* (B), *12247* (U), *12290* (B). Gandoca-Manzanillo Wildlife Refuge, Manzanillo Section (La Amistad Caribe Conservation Area), Manzanillo, 170 km ESE of San José, 65 km SE of Limón, trail along beach; 82° 53' W, 9° 38' N, sea level; lowland coastal moist forest zone, disturbed coastal vegetation with *Cocos nucifera*, *Coccoloba uvifera*, and *Rhizophora mangle*, on bark (stump) of *Cocos nucifera*, semi-exposed; Mar 2004, *Aptroot 60307* (BR), *Nelsen 3721f* (INB, WIS), *Sipman 51711* (B, INB), *51720* (B, INB), *Trest 1527b*, *c* (INB, hb. Trest), *Will-Wolf* 12724b (CR, INB, WIS); ibid., on bark (lower trunk), fully shaded; Mar 2004, *Lücking 17097b* (F, INB); ibid., on bark of *Ficus*; Mar 2004, *Lücking 17100b* (F, INB); ibid., on bark of *Terminalia catappa*; Mar 2004, *Aptroot 60366* (BR). Puntarenas: Corcovado National Park (Osa Conservation Area), Sirena Biological Station, beach E of airstrip; 83° 36' W, 8° 28' N, sea level; disturbed coastal forest and exposed trees along beach, on thin, well-lit trunk; Apr 2003, *Sipman 51112* (B, INB). Manuel Antonio National Park, near Quepos; 84° 09' W, 9° 23' N, sea level; scattered trees around hotel at end station of bus line; Nov 1988, *Sipman 42271* (B, CR), *42309* (B, CR); Manuel Antonio National Park (Pacífico Central Conservation Area),

65 km S of San José, trail along beach; 84° 09' W, 9° 25' N, sea level; lowland coastal moist forest zone, disturbed coastal moist forest, on bark (lower trunk), semi-exposed; Apr 1991, *Lücking s.n.* (F). Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk) of *Cocos nucifera*, semi-exposed; Feb 1997, *Lücking 97-109*, *97-120b*, *97-155*, *97-188* (F).

***Leucodecton compunctellum* (Nyl.) Frisch** (Fig. 14E)

Leucodecton compunctellum (Nyl.) Frisch, Biblioth. Lichenol. 92: 155 (2006); *Thelotrema compunctellum* Nyl., Bull. Soc. Linn. Normandie, Sér. 2, 2: 77 (1868); *Leptotrema compunctellum* (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 632 (1923). Lectotype (Hale 1972; Mangold *et al.* 2009: 248). New Caledonia, *Thiébault s.n.* (H-NYL 22703!).

Thelotrema monosporum var. *subgemium* Nyl., Bull. Soc. Linn. Normandie, Sér. 2, 2: 77 (1868); *Thelotrema subgemium* (Nyl.) Nyl., Sert. Lich. Trop. Labuan Singapore: 5 (1891). Lectotype (Hale 1972; Mangold *et al.* 2009: 248). New Caledonia, *Thiébault s.n.* (H-NYL 22702!).

Thelotrema elachistoteron Leight., Trans. Linn. Soc. London 27: 169 (1870); *Leptotrema elachistoteron* (Leight.) Patw. & C. Kulk., Norw. J. Bot. 24: 128 (1977); *Myriotrema elachistoteron* (Leight.) Hale, Mycotaxon 11: 133 (1980); *Leucodecton elachistoteron* (Leight.) Frisch, Biblioth. Lichenol. 92: 155 (2006). Lectotype (Hale 1981: 278). Sri Lanka, *Thwaites s.n.* (BM!).

Thelotrema reclusum Kremp. in Nylander, Bull. Soc. Linn. Normandie, Sér. 2, 7: 168 (1873); *Leptotrema reclusum* (Kremp.) Zahlbr., Cat. Lich. Univ. 2: 639 (1923); *Myriotrema reclusum* (Kremp.) Hale, Mycotaxon 11: 135 (1980). Lectotype (Hale 1978: 54). India (Andaman Islands), *Kurz 21* (M!; isolectotype: BM!).

Anthracothecium oligosporum Müll. Arg., Flora 71: 48 (1888); *Leptotrema oligosporum* (Müll. Arg.) Patw. & Makhija, Bryologist 83: 368 (1980). Lectotype (Patwardhan & Makhija 1980: 368). Australia, *Wickham s.n.* (G!).

Thelotrema microglaenoides Vain., J. Bot. 34: 206 (1896) [non *T. microglaenoides Vain*., Ann. Univ. Fenn. Åbo, Ser. A, 2(3): 32 (1926); nom. illeg.]; *Leptotrema microglaenoides* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 637 (1923). Holotype. St Vincent, *Elliott 266* (TUR-VAIN 26773!; isotype: BM!).

Leptotrema deceptum Hale, Smithson. Contr. Bot. 16: 39 (1974); *Myriotrema deceptum* (Hale) Hale, Mycotaxon 11: 133 (1980). Holotype. Lesser Antilles (Dominica), *Hale 37860* (US!).

Thallus light grey-olive-yellow, with minutely grainy surface, with loose cortex; photobiont layer and medulla with columnar clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.2–0.4 mm diam.; disc concealed by minute, ostiolate, 0.03–0.05 mm wide pore, invisible; margin entire, brown, forming brown spot around ostiole. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids absent. Hymenium 150–200 µm high, clear; paraphyses unbranched. Ascospores 1–4/ascus, richly muriform, 60–130 15–35 µm, ellipsoid, with slightly thickened septa and rectangular lumina, brown, young weakly I+ violet-blue (amyloid). Secondary chemistry: stictic, constictic, hypostictic, and hypoconstictic acids.

Remarks:—This species is very similar to *Leucodecton bisporum* but differs in the clear hymenium and the slightly smaller ascospores. Also similar is *Leucodecton sordidescens* (see below), which has much smaller ascospores. *Leucodecton compunctellum* has an extensive synonymy (Frisch 2006; Mangold *et al.* 2009; Rivas Plata *et al.* 2010a), but is in fact rather uniform in thallus and apothecial morphology.

Specimens examined:—COSTA RICA. Puntarenas: Along trail towards Corozal; 5–50 m; Apr 1930, *Dodge 7806* [FH; as *Leptotrema leucocarpoides* (Leight.) Zahlbr.]. Cordillera de Tilarán, Monteverde, surroundings of the Hotel de la Montana; 1500 m; lower montane rain forest zone; Apr 1979, *Kalb & Plöbst 32990* (hb. Kalb).

***Leucodecton compunctum* (Ach.) A. Massal.** (Fig. 13F)

Leucodecton compunctum (Ach.) A. Massal., Atti Reale Ist. Veneto Sci. Lett. Arti, Ser. 3(5): 326 (1860); *Porina compuncta* Ach., Syn. Meth. Lich.: 112 (1814). Lectotype (Frisch 2006: 148): West Indies, s.col. (H-ACH 734!; specimen 1a).

Thelotrema pauperculum Vain., Mycologia 20: 37 (1929). Holotype. Puerto Rico, *Fink 519* (TUR-VAIN 33203!).

Thallus grey-olive-yellow, smooth, with dense, prosoplectenchymatous cortex; photobiont layer and/or medulla with irregular (not columnar) clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.2–0.4 mm diam.; disc concealed by minute, ostiolate, 0.03–0.05 mm wide pore, invisible; margin entire, brown. Columella absent. Excipulum paraplectenchymatous, brown; periphysoids absent. Hymenium 120–150 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, muriform, 25–35 × 15–18 µm, ellipsoid, with thickened septa and rounded lumina, colorless to pale brown, young I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This species has been much confused in the literature (Rivas Plata *et al.* 2010a). Even in our recent key, where it was given as having variable chemistry (nil or stictic acid and satellite substances). As noted by Frisch (2006), the type has no lichen substances, and material with stictic acid possibly belongs in *Wirthiotrema* (see below). *Leucodecton compunctum* s.str. has a smooth thallus with dense cortex, lacking the minutely grainy surface characteristic of many other species. It closely resembles a *Porina* and it is no surprise that it was originally described in that genus. The only other species in the genus lacking substances and with small, brown, muriform ascospores is *L. desquamescens* (Vain.) Rivas Plata & Lücking, which has a grainy thallus with columnar clusters of crystals and much larger apothecia with exposed disc and double margin resembling those of *L. glaucescens*. Otherwise most similar to L. compunctum is *L. fissurinum* (see below), which produces stictic acid and has myriotremoid apothecia with a brown spot around the ostiole.

Specimens examined:—COSTA RICA. Puntarenas: Fila Cruces Ridge, surroundings of Las Cruces Tropical Botanical Garden, 4 km SSE of San Vito; 8° 43' N, 82° 58' W, 1550 m; in a premontane rainforest at a waterfall; Jan 1979, *Kalb & Plöbst 38932* (hb. Kalb).

Leucodecton dactyliferum* (Hale) Lücking, *comb. nov.
MycoBank #800057

Ocellularia dactylifera Hale, Smithson. Contr. Bot. 38: 19 (1978); *Myriotrema dactyliferum* (Hale) Hale, Mycotaxon 11: 133 (1980). Holotype. Panama, *Hale 43503* (US!).

Thallus light grey-green, verrucose, producing coarse isidia, with loose cortex; isidia up to 0.5 mm long; photobiont layer and medulla with irregular (not columnar) clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.1–0.15 mm diam.; disc covered by narrow, 0.05–0.1 mm wide pore, invisible; margin entire, fused, pale brown, white-pruinose. Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 12–16 × 4–6 µm, 3–7-septate, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: stictic and constictic acids.

Remarks:—Because of thallus and excipular structure and chemistry, this species is here placed in *Leucodecton*, but this has to be tested by molecular data. No other species of *Leucodecton* has isidia.

Specimens examined:—Not yet known from Costa Rica, but reported from Panama (Hale 1978).

***Leucodecton expallescens* (Nyl.) Rivas Plata & Lücking** (Fig. 14G)

Leucodecton expallescens (Nyl.) Rivas Plata & Lücking, Lichenologist 42: 184 (2010); *Thelotrema expallescens* Nyl., *Flora* 59: 560 (1876). Holotype. Cuba, *Wright s.n.* (H-NYL!; isotype: US!; Wright, Lich. Cub. 86).

Thallus light yellow-grey, smooth to uneven, with loose cortex; photobiont layer and medulla with irregular (not columnar) clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.3–0.4 mm

diam.; disc partially covered by 0.15–0.25 mm wide pore, grey-brown, white-pruinose; margin entire, white, proper excipulum free (double margin). Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 4–8/ascus, submuriform with 5–7 transverse septa and 0–2 longitudinal septa per segment, 12–20 × 6–8 µm, ellipsoid, with thin to slightly thickened septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: stictic, constictic, hypoconstictic, and hypostictic acids.

Remarks:—This species was combined in the genus *Leucodecton* because the type agrees in several features with that genus, including thallus morphology and anatomy, the paraplectenchymatous excipulum lacking periphysoids, and the chemistry (Rivas Plata *et al.* 2010a). However, material included here (*Lücking 15069*) clusters with *Myriotrema peninsulae* R. C. Harris and *Nadvornikia hawaiiensis* in molecular phylogenetic analyses, separate from *Leucodecton* (Rivas Plata & Lumbsch 2011a). It is at present unclear whether this species should be excluded from *Leucodecton* entirely or whether the material represents more than one species, partly belonging in *Leucodecton* and partly related to *Nadvornikia*. Sequences from at least two more collections are needed to elucidate this problem, and for the time being we retain all material in *Leucodecton expallescens*.

Specimens examined:—COSTA RICA. Guanacaste: Cacao Biological Station (Guanacaste Conservation area); 85° 28' W, 10° 56' N, 1000 m; epiphyte in humid primary montane forest near the station; Jun 1995, *Sipman 37291* (B, CR). Puntarenas: Cordillera de Tilarán, Monteverde, near the cheese factory; 84° 49' W, 10° 18' N, 1450 m; premontane rain forest zone, forest relics among pasturefields, on trunks; Jan 1979, *Sipman 12104* (U), *12174* (U). Monteverde, surroundings of the Hotel de la Montaña; 1500 m; lower montane rain forest; Jan 1979, *Kalb & Plöbst s.n.* (hb. Kalb). Las Tablas Protection Zone, Cedro Ridge, Las Alturas Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km NE of San Vito near Alturas, surroundings of station and trail into forest; 82° 50' W, 8° 57' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower stem), fully shaded; Jun 2002, *Lücking 15069* (INB); ibid., La Neblina Section (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km ENE of San Vito near Las Mellizas, access road to fincas; 82° 45' W, 8° 55' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (trunk, fallen), semi-exposed; Jun 2002, *Lücking 15123* (F, INB); ibid., on bark (lower stem), partially shaded; Jun 2002, *Sipman 47892* (B, INB).

***Leucodecton fissurinum* (Hale) Frisch** (Fig. 14H)

Leucodecton fissurinum (Hale) Frisch, Biblioth. Lichenol. 92: 156 (2006); *Myriotrema fissurinum* Hale, Bull. Br. Mus. Nat. Hist. (Bot.) 8(3): 279 (1981). Holotype. Sri Lanka, *Hale 46227* (US!; isotype: BM!).

Thallus light grey-olive, smooth, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with irregular (not columnar) clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.4–0.8 mm diam.; disc concealed by small, 0.05–0.1 mm wide pore, invisible; margin entire, brown, forming brown spot around ostiole. Columella absent. Excipulum paraplectenchymatous, pale brown; periphysoids absent. Hymenium 100–140 µm high, clear; paraphyses unbranched. Ascospores 4–8/ascus, muriform, 20–35 × 10–15 µm, ellipsoid, with thickened septa and rounded lumina, colorless to pale brown, young I+ violet-blue (amyloid). Secondary chemistry: stictic, constictic, hypostictic, hypoconstictic, and α-acetylconstictic acids.

Remarks:—This species belongs in the *Leucodecton compunctum* aggregate, but differs from *L. compunctum* in the loose cortex and myriotremoid rather than porinoid apothecia, with distinct brown spot around the ostiole, in addition to the chemistry. *Leucodecton subcompunctum* (see below) shares with *L. fissurinum* the dense thallus cortex and chemistry but has immersed-lepadinoid apothecia with free excipulum and double margin and smaller ascospores. The newly described *L. album* (see above) has a whitish thallus and smaller, more dense and prominent ascocarps with completely closed pores. *Leucodecton sordidescens*

(see below) agrees with *L. fissurinum* in most aspects except for the grainy thallus caused by columnar clusters of calcium oxalate crystals, and the loose cortex. Contrary to the epithet, a fissured thallus is not a diagnostic feature of *L. fissurinum*, but depends on the substrate and thallus thickness.

Specimens examined:—COSTA RICA. Guanacaste: Volcán Tenorio National Park, Alto Masis Section (Arenal-Tilarán Conservation Area), Tilarán Ridge, 125 km NW of San José, 15 km NNW of Tilarán, near Tierras Morenas, surroundings of station; 85° 00' W, 10° 37' N, 950–1000 m; lower montane elfin cloud forest zone, disturbed low elfin forest and secondary vegetation, on bark (lower stem), exposed; Mar 2004, *Aptroot 60598*, *60606*, *60611* (BR), *Sipman 51923* (B, INB).

***Leucodecton glaucescens* (Nyl.) Frisch** (Fig. 15A)

Leucodecton glaucescens (Nyl.) Frisch, Biblioth. Lichenol. 92: 164 (2006); *Thelotrema glaucescens* Nyl., Ann. Sci. Nat. Bot., Ser. 4, 19: 332 (1863); *Leptotrema glaucescens* (Nyl.) Müll. Arg., Flora 65: 499 (1882); *Myriotrema glaucescens* (Nyl.) Hale, Mycotaxon 11: 133 (1980). Lectotype (Hale 1981: 282): U.S.A., *Hale s.n.* (FH!).

Thallus light grey-olive, smooth to uneven, typically gall-forming, with loose cortex; photobiont layer and medulla with columnar clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, aggregate to pseudostromatic, 0.2–0.3 mm diam.; disc more or less exposed, brown-black, white-pruinose; margin finely lobulate, with split between thallus and proper margin, white-grey to pale brown. Columella absent. Excipulum paraplectenchymatous, brown; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–1 longitudinal septa per segment, 12–18 × 6–10 µm, ellipsoid, with thickened septa and rounded lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: stictic, constictic, cryptostictic, and hypostictic acids.

Remarks:—Because of its gall-forming thallus and minutely chroodiscoid apothecia, this species somewhat resembles *Reimnitzia santensis* (see below), which has a similar thallus but much larger, distinctly chroodiscoid apothecia. A characteristic feature of *Leucodecton glaucescens* is the aggregation of the apothecia into often pseudostromatic areas.

Specimens examined:—COSTA RICA. Guanacaste: Upper slopes of Cerro San José de Líbano; 500–960 m; Feb 1930, *Dodge et al. 6696* (FH; as *Leptotrema polyporum* Riddle). Limón: Gandoca-Manzanillo Wildlife Refuge, Manzanillo Section (La Amistad Caribe Conservation Area), Manzanillo, 170 km ESE of San José, 65 km SE of Limón, trail along beach; 82° 53' W, 9° 38' N, sea level; lowland coastal moist forest zone, disturbed coastal vegetation with *Cocos nucifera*, *Coccoloba uvifera*, and *Rhizophora mangle*, on bark (lower trunk) of *Ficus*, partially shaded; Mar 2004, *Lücking 17100d* (F, INB). Puntarenas: Monte Verde, Cordillera de Tilaran, ca. 20 km E of Juntas; Jan 1979, *Filson 16381a* (MEL).

***Leucodecton occultum* (Eschw.) Frisch** (Fig. 15B)

Leucodecton occultum (Eschw.) Frisch, Biblioth. Lichenol. 92: 157 (2006); *Thelotrema occultum* Eschw. in Martius, Fl. Bras. 1: 174 (1833); *Leptotrema occultum* (Eschw.) Hale, Smithson. Contr. Bot. 16: 40 (1974); *Myriotrema occultum* (Eschw.) Hale, Mycotaxon 11: 134 (1980). Holotype. Brazil, s.col. (M!; isotype: G!).

Urceolaria compuncta Ach., Meth. Lich.: 143 (1803) [non *Porina compuncta* Ach., Syn. Meth. Lich.: 112 (1814). ≡ *Leucodecton compunctum* (Ach.) A. Massal.]; *Leptotrema compunctum* (Ach.) Müll. Arg., Flora 71: 527 (1888); *Leptotrema compactum* (Ach.) Müll. Arg., Flora 70: 400 (1887) [orth. error for *L. compunctum*]; *Myriotrema compunctum* (Ach.) Hale, Mycotaxon 11: 133 (1980). Lectotype (Hale 1981: 276): Indonesia, *Smith s.n.* (LINN-Sm 1692.7, not seen; isolectotypes: G!, H-NYL 22447!).

Leptotrema compunctum var. *purpuratum* Müll. Arg., Bull. Soc. Roy. Bot. Belgique 30: 75 (1891). Holotype. Costa Rica, *Tonduz s.n.* (G!; isotype: US!; Pittier, Pl. Costaric. Exs. 5218).

Thelotrema loandense Vain., Cat. Welwitsch. Afr. Pl. 2(2): 429 (1901); *Leptotrema loandense* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 636 (1923). Holotype. Angola, *Welwitsch 441* (TUR-VAIN 26793!; isotype: BM!).

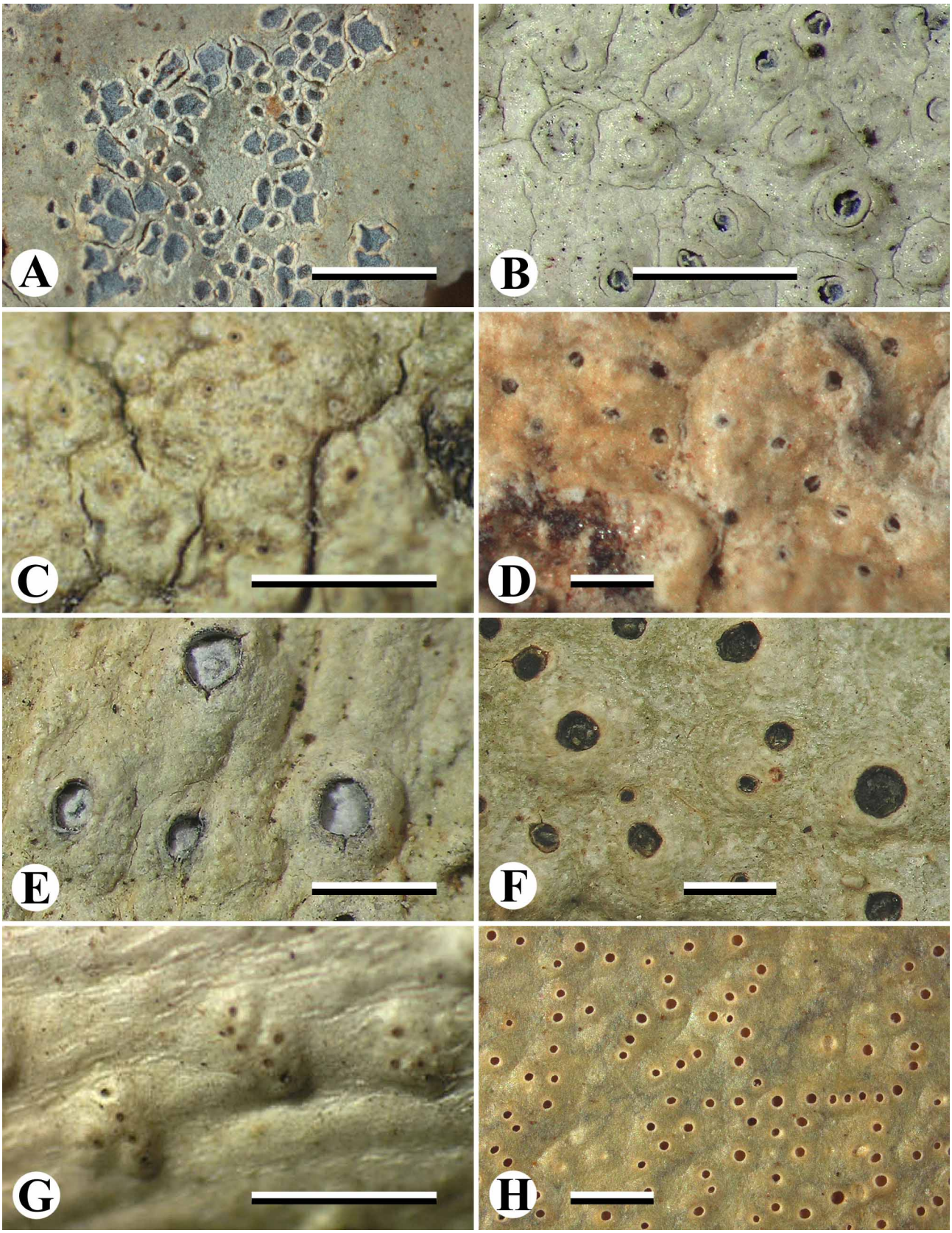

FIGURE 15. A. *Leucodecton glaucescens*. B. *Leucodecton occultum*. C. *Leucodecton sordidescens*. D. *Leucodecton subcompunctum*. E. *Melanotrema meiospermum*. F. *Melanotrema platystomum*. G. *Myriotrema aggregans*. H. *Myriotrema album*. Scale = 1 mm.

Thelotrema compunctum var. *antillarum* Vain., Ann. Acad. Sci. Fenn., Ser. A, 6(7): 134 (1915); *Thelotrema* '*bahianum*' var. *antillarum* Vain. in Zahlbr., Catal. Lich. Univ. 2: 633 (1923), orth. error; *Leptotrema compunctum* var. *antillarum* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 633 (1923). Lectotype (Salisbury 1971: 276). Virgin Islands, *Raunkiaer 553* (TUR-VAIN 26798!).

Thelotrema compunctum var. *praiense* Vain., Bol. Soc. Brot., Sér. 2, 6: 149 (1929). Holotype. Mozambique, *Pires de Lima 383* (TUR-VAIN 34802!).

Thelotrema compunctum f. *portoricensis* Vain., Mycologia 21: 38 (1929); *Leptotrema compunctum* f. *portoricense* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 632 (1923). Holotype. Puerto Rico, *Fink 1749* (W!; isotype: NY!).

Thallus light yellow-grey, smooth to uneven, ecorticate; photobiont layer and medulla with irregular (not columnar) clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.2–0.3 mm diam.; disc more or less exposed, brown-black, white-pruinose; margin entire, with split between thallus and proper margin (double margin), pale brown. Columella absent. Excipulum paraplectenchymatous, brown; periphysoids absent. Hymenium 90–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 5–7 transverse septa and 0–2 longitudinal septa per segment, 20–30 × 8–12 µm, ellipsoid, with thickened septa and rounded lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: norstictic acid.

Remarks:—*Leucodecton occultum* resembles a minute *Thelotrema* because of its lepadinoid apothecia with double margin. This feature, together with the presence of norstictic acid, make the species unmistakable. The long list of synonyms is therefore surprising. The type of *Leucodecton compunctum* var. *purpuratum*, described from Costa Rica (Müller 1891), has an intense purple thallus, suggesting the presence of an anthraquinone. However, a spot test was negative for anthraquinones and instead revealed norstictic acid; possibly, the color results from massive decomposition of the latter due to improper drying of the material. *Leucodecton occultum* appears to be one of the few thelotremoid Graphidaceae characteristic of drier habitats.

Specimens examined:—COSTA RICA. Guanacaste: Barra Honda National Park, Barra Honda Biological Station (Tempisque Conservation Area), Barra Honda Mountains, 140 km WNW of San José, 10 km ENE of Nicoya, main trail to Terciopelo cave and Mirador; 85° 21' W, 10° 10' N, 400–500 m; lowland to lower montane moist forest zone, disturbed primary and oldgrowth secondary forest with calcareous rock outcrops, on bark (lower trunk), semi-exposed; Mar 2004, *Aptroot 60844* (BR), *Sipman 52035*, *52040a* (B, INB), *Will-Wolf 12834b* (CR, INB, WIS). Carretera Regional 151, 5 km E of Coco, 30 km W of Liberia; 85° 40' W, 10° 33' N, 50 m; canopy of fallen tree; Jan 1979, Hafellner s.n. (hb. Kalb; Kalb, Lich. Neotrop. 432). Lomas de Barbudal Biological Reserve, Lomas de Barbudal Station (Tempisque Conservation Area), Río Tempisque Bassin, 140 km WNW of San José and 20 km WSW of Bagaces, trail from station to Río Barbudal; 85° 22' W, 10° 30' N, 100 m; lowland to lower montane moist forest zone, disturbed gallery forest and forest remnants, on bark (lower trunk), semi-exposed; Mar 2003, *Lücking 16100a* (CR, F, INB, hb. Kalb); ibid., on bark (stem), Mar 2003, *Sipman 51046c* (B, CR). Palo Verde National Park, Palo Verde Station (Tempisque Conservation Area), Río Tempisque Bassin, 130 km WNW of San José and 30 km SSW of Bagaces, trail west of station parallel to Río Tempisque; 85° 23' W, 10° 22' N, 10 m; lowland to lower montane moist forest zone, disturbed open primary and secondary forest, on bark (lower trunk), semi-exposed; Mar 2003, *Trest 1312a* (INB, WIS); ibid., lower part of Guayacan trail; 85° 21' W, 10° 21' N, 10–50 m; disturbed primary, dry, deciduous forest, on thin trunk; Mar 2003, *Sipman 50983b* (B, INB). Río San José, upper portion of cañon; Feb 1930, *Dodge & Thomas 6925* (FH; as *Leptotrema develatum* (Nyl.) Zahlbr.).

Leucodecton sordidescens* (Fée) Lücking & Sipman, *comb. nov. (Fig. 15C)
MycoBank #800068

Trypethelium sordidescens Fée, *Essai Crypt. Exot.*, Suppl. (Paris) 2: 64 (1837); *Thelotrema sordidescens* (Fée) Nyl., *Mém. Soc. Imp. Sci. Nat. Cherbourg* 5: 118 (1857); *Myriotrema sordidescens* (Fée) Kalb, *Herzogia* 9: 75 (1992). Holotype: Brazil, *Glaziou 190* (G!; isotype: M!).

Thelotrema subsphaerosporum Harm., *Bull. Séanc. Soc. Sci. Nancy*, Sér. 3, 13: 38 (1912); *Leptotrema subsphaerosporum* (Harm.) Zahlbr., *Cat. Lich. Univ.* 2: 640 (1923). Holotype: New Caledonia, *Pionniero s.n.* (DUKE!).

Thallus grey-olive-yellow, with minutely grainy surface, with loose cortex; photobiont layer and/or medulla with columnar clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.3–0.5 mm diam.; disc concealed by minute, ostiolate, 0.03–0.05 mm wide pore, invisible; margin entire, brown. Columella absent. Excipulum paraplectenchymatous, brown; periphysoids absent. Hymenium 120–150 µm high, clear; paraphyses unbranched. Ascospores 4–8/ascus, muriform, 25–35 × 15–18 µm, ellipsoid, with thickened septa and rounded lumina, colorless to pale brown, young I+ violet-blue (amyloid). Secondary chemistry: stictic, hypostictic, cryptostictic, and constictic acids.

Remarks:—This species resembles *Leucodecton bisporum* and *L. compunctellum* morphologically, particularly in the grainy thallus with columnar crystal clusters, but differs in the much smaller ascospores. Regarding ascospore dimensions, it comes closest to *L. compunctum* and relatives, which differ all morphologically and in part chemically: *L. compunctum* by a dense cortex and porinoid ascomata and lacking lichen substances; *L. fissurinum* by irregular (not columnar) crystal clusters and smooth to uneven surface with dense cortex; *L. phaeosporum* (Nyl.) Rivas Plata & Lücking by a gall-forming thallus with immersed apothecia lacking a brown spot around the ostiole, and smaller ascospores; and *L. subcompunctum* (Nyl.) Frisch by a densely corticate, smooth thallus and minutely lepadinoid apothecia with free excipulum and double margin.

Specimens examined:—COSTA RICA. Guanacaste: Cacao Biological Station (Guanacaste Conservation area); 85° 28' W, 10° 56' N, 1000 m; epiphyte in humid primary montane forest near the station; Jun 1995, *Sipman 37288* (B, CR). Limón: Caribbean coast, S of Cahuita; 82° 50' W, 9° 44' N, sea level; *Cocos* trunks in orchard immediately S of the town; Jan 1979, *Sipman 12243* (B), *12250* (B). Gandoca-Manzanillo Wildlife Refuge, Manzanillo Section (La Amistad Caribe Conservation Area), Manzanillo, 170 km ESE of San José, 65 km SE of Limón, trail along beach; 82° 53' W, 9° 38' N, sea level; lowland coastal moist forest zone, disturbed coastal vegetation with *Cocos nucifera*, *Coccoloba uvifera*, and *Rhizophora mangle*, on bark of *Terminalia catappa*; Mar 2004, *Aptroot 60360* (BR); ibid., on bark (lower trunk) of *Cocos nucifera*, exposed; Mar 2004, *Sipman 51710* (B, INB). Puntarenas: Cordillera de Tilaran, Monteverde, near the cheese factory; 84° 49' W, 10° 18' N, 1450 m; premontane rain forest zone, forest relics among pasturefields, on trunks; Jan 1979, *Sipman 12081* (B). Manuel Antonio National Park, near Quepos; 84° 09' W, 9° 23' N, sea level; scattered trees around hotel at end station of bus line; Nov 1988, *Sipman 42270a* (B, CR).

MASCARENES. La Réunion; 55° 40' W, 21° 10' S; Apr 1989, *Follmann & Follmann-Schrag s.n.* (B). SEYCHELLES. Aldabra, Cinc Cases; on *Mytroxylon aethiopicum*; Sep 1973, *Hnatiuk s.n.* (B).

***Leucodecton subcompunctum* (Nyl.) Frisch** (Fig. 15D)

Leucodecton subcompunctum (Nyl.) Frisch in Frisch *et al.*, Biblioth. Lichenol. 92: 162 (2006); *Thelotrema subcompunctum* Nyl., Bull. Soc. Linn. Normandie, Sér. 2, 2: 76 (1868); *Leptotrema subcompunctum* (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 640 (1923); *Myriotrema subcompunctum* (Nyl.) Hale, Mycotaxon 11: 135 (1980). Lecotype (Hale 1974: 42). New Caledonia, *Thiébaut s.n.* (H-NYL 22440!; isolectotype: G!).
Leptotrema diffractum Müll. Arg., Hedwigia 30: 50 (1891). Holotype. Australia, *Bailey 527* (G!).
Leptotrema polycarpum Müll. Arg., Bull. Herb. Boiss. 3: 315 (1895). Holotype: Australia, comm. Knight (G!).
Leptotrema inclusum Zahlbr., Bot. Mag. Tokyo 41: 317 (1927). Holotype. Japan, *Faurie 5147* (W!).
Myriotrema decorticatum Hale, Bull. Brit. Mus. Nat. Hist., Bot. Ser., 8: 277 (1981). Holotype: Sri Lanka, *Hale 46259* (US!).

Thallus light olive-grey, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with irregular clusters of calcium oxalate crystals. Apothecia immersed-erumpent, rounded, 0.2–0.4 mm diam.; disc covered by 0.1–0.2 mm wide pore, brown-black, white-pruinose; margin entire, with split between thallus and proper margin (double margin), brown. Columella absent. Excipulum paraplectenchymatous, brown; periphysoids absent. Hymenium 90–120 µm high, clear; paraphyses unbranched. Ascospores 4–8/ascus, muriform, 15–25 × 9–15 µm, ellipsoid, with thickened septa and rounded

lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: stictic, constictic, α-acetyl-constictic, and hypostictic acids.

Remarks:—Like *Leucodecton occultum* (see above), *L. subcompunctum* resembles a minute *Thelotrema* because of its lepadinoid apothecia with double margin. The main differences between the two species are the dense cortex and stictic acid chemistry present in *L. subcompunctum*.

Specimens examined:—COSTA RICA. Guanacaste: N of the Carretera Regional 151, 5 km E of Coco, 30 km W of Liberia; 85° 40' W, 10° 33' N, 50 m; canopy of fallen tree; Jan 1979, Hafellner s.n. (GZU; Kalb, Lich. Neotrop. 432). Guanacaste: Palo Verde National Park, Palo Verde Station (Tempisque Conservation Area), Río Tempisque Bassin, 130 km WNW of San José and 30 km SSW of Bagaces, lower parts of Guayacan trail; 85° 21' W, 10° 21' N, 10–50 m; lowland to lower montane moist forest zone, disturbed primary forest remnants and open secondary forest, on bark (lower trunk), semi-exposed; Mar 2003, *Buck 43916*, *43941* (INB, NY).

Melanotrema Frisch

Melanotrema Frisch in Frisch & Kalb, Biblioth. Lichenol. 93: 382 (2006). Type. *Melanotrema platystomum* (Mont.) Frisch.

Thallus light grey-olive to yellow-grey, with loose cortex or rarely ecorticate or with dense cortex. Apothecia erumpent to prominent, angular-rounded to elongate-lirellate; disc partially covered; margin entire to fissured or rarely lobulate, fused or free. Columella present, broad-stump-shaped to irregular or reticulate, carbonized. Excipulum prosoplectenchymatous, carbonized (rarely brown); periphysoids absent. Paraphyses unbranched. Ascospores septate to submuriform, ellipsoid to oblong, with thick septa and lens-shaped lumina, colorless to mostly (dark) brown, I+ violet-blue (amyloid) in colorless or young ascospores. Secondary chemistry: no substances or stictic acid or lichexanthone, rarely protocetraric or psoromic acid.

Remarks:—*Melanotrema* is one of the recent segregates of *Ocellularia* s.lat. established by Frisch & Kalb (2006). It is characterized by the usually loosely corticate thallus containing mostly stictic acid, lichexanthone, or no substances, and the irregularly chroodiscoid apothecia with broad stump-shaped to irregular-reticulate columella. Most similar are species in *Redingeria* and *Stegobolus* s.lat., such as *Redingeria glaucoglyphica* (Sipman) Frisch and *Stegobolus metaphoricus* (see below), and the morphological distinction of the three genera is not clearcut (Frisch & Kalb 2006). Molecular data suggest that the core group of *Melanotrema*, comprising *M. meiospermum* and relatives, is genetically distinct from both *Redingeria* and *Stegobolus* s.lat. (Rivas Plata *et al.* 2012b), and morphologically intermediate species need to be sequenced to assertain their correct phylogenetic relationships. For instance, the species described as *Leptotrema microsporum* morphologically best fits into *Melanotrema* but genetically belongs in *Redingeria*, as *R. microspora* (see below). Another genus to be easily confused with *Melanotrema* is *Clandestinotrema*, which includes species such as *C. stylothecium* (see above) that agree in thallus and apothecial morphology with *Melanotrema*, but have I-negative, trypethelioid ascospores with diamond-shaped lumina (Rivas Plata & Lumbsch 2011a).

Key to the species of *Melanotrema* found or expected in Costa Rica (2)

2. Ascospores persistently colorless ..... ***M. platystomum***
- Ascospores becoming brown ..... ***M. meiospermum***

***Melanotrema meiospermum* (Nyl.) Frisch** (Fig. 15E)

Melanotrema meiospermum (Nyl.) Frisch in Frisch & Kalb, Biblioth. Lichenol. 92: 394 (2006); *Thelotrema meiospermum* Nyl., Ann. Sci. Nat. Bot., Ser. 4, 19: 333 (1863); *Phaeotrema meiospermum* (Nyl.) Müll. Arg., Flora 69: 311 (1886); *Ocellularia meiosperma* (Nyl.) Hale, Mycotaxon 11: 137 (1980). Holotype. Cuba, *Wright s.n.* (H-NYL 22856!; Wright, Lichenes Cubae 136).

Thallus light grey-olive, smooth to uneven, with loose cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.5–1 mm diam.; disc partially covered by 0.3–0.7 mm wide pore, filled by brown-black, white-pruinose columella; margin fissured, fused, brown-black, felty white-pruinose. Columella present, broad-stump-shaped, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–7-septate, 15–25 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This species displays the typical characteristics of the genus, with a loose cortex, no substances, and melanotremoid apothecia with broad columella. It closely resembles *Clandestinotrema leucomelaenum* (see above) and can only be separated by the different ascospore type. *Melanotrema meiospermoides* (Hale) Frisch is closely related but has apothecia with a narrow pore and slightly larger ascospores. *Melanotrema platystomum* (see below) differs chiefly in the persistently colorless ascospores.

Specimens examined:—Not yet found in Costa Rica but reported from Panama (Hale 1978).

***Melanotrema platystomum* (Mont.) Frisch** (Fig. 15F)

Melanotrema platystomum (Mont.) Frisch in Frisch & Kalb, Biblioth. Lichenol. 92: 397 (2006); *Thelotrema platystomum* Mont., Ann. Sci. Nat. Bot., Ser. 2, 19: 79 (1843); *Ocellularia platystoma* (Mont.) Zahlbr., Cat. Lich. Univ. 2: 598 (1923). Holotype. French Guiana, *Leprieur 491* (PC!; isotype: H-NYL 22795!).

Ocellularia concolor Meyen & Flotow, Nova Acta Acad. Leopold.-Carol. 19, Suppl.: 230 (1843). Type: Philippines, *Meyen s.n.* (G!).

Thallus light grey-olive, smooth to uneven, with loose cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.5–1 mm diam.; disc partially covered by 0.3–0.5 mm wide pore, filled by brown-black, white-pruinose columella; margin fissured, fused, brown-black, felty white-pruinose. Columella present, broad-stump-shaped, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–9-septate, 16–25 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Melanotrema platystomum* is identical to *M. meiospermum* in all characters except the persistently colorless ascospores. Hale (1978) reported the species from Panama as *Ocellularia concolor.*

Specimens examined:—COSTA RICA. Alajuela: Maquenque Mixed National Wildlife Refuge, Huetar Norte; 84° 11' W, 10° 42' N, 0–100 m; Apr 2005, *Chaves 2353* (INB). Puntarenas: La Amistad International Park, Altamira Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 20 km N of San Vito near Finca Colorado, trail to Casa Coca; 82° 59' W, 9° 02' N, 1800 m; montane rain forest zone, abandoned pasture with forest remnants, on bark (lower trunk), semi-exposed; Jul 2002, *Sipman 48065a*, *d* (B, INB).

Myriotrema Fée

Myriotrema Fée, Méth. Lichénograph. Gen.: 34 (1824). Type. *Myriotrema olivaceum* Fée.

Thallus usually light grey-olive, smooth to uneven or verrucose to rarely bullate, usually with dense, prosoplectenchymatous cortex, rarely ecorticate or with loose cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed to prominent, rounded to angular-rounded; disc covered by more or less narrow pore; margin usually entire, fused or free, laterally covered by thalline layer. True columella absent, but irregular pseudocolumella above the hymenium and extending from the lateral excipulum sometimes present, or fenestrate excipulum resembling a columella, uncarbonized and white. Excipulum prosoplectenchymatous, colorless to rarely brown; periphysoids absent. Paraphyses unbranched. Ascospores transversely septate to muriform, small to large, ellipsoid-fusiform to oblong-cylindrical, with thick septa and lens-shaped lumina (except in richly muriform ascospores), colorless or rarely brown, I+ violet-blue (amyloid). Secondary chemistry: variable, frequently psoromic acid or protocetraric acid or relatives and satellite substances.

Remarks:—*Myriotrema* was first characterized in a modern sense by Hale (1980), who included all species with uncarbonized excipulum and lacking periphysoids in this genus. Frisch (2006) refined this concept, retaining in *Myriotrema* basically those species with myriotremoid apothecia (small pores), a prosoplectenchymatous cortex often with internal splitting, and I+ violet-blue (amyloid) ascospores. Other species were segregated into genera such as *Leucodecton* (Frisch 2006) and *Wirthiotrema* (Rivas Plata *et al.* 2010b). Chemistry appears to play a significant role in generic assignment, since all species with stictic acid turned out to be unrelated to *Myriotrema* s.str. (Rivas Plata *et al.* 2010a). The molecular data now available indicate that even *Myriotrema* s.str., i.e. sensu Frisch (2006), is an artificial taxon, including species that are related to other groups. For example, *M. glaucophaenum* forms a separate clade and *M. laeviusculum* is related to *Ocellularia bahiana* (Rivas Plata *et al.* 2012b). Since this is currently under investigation, we have here chiefly retained the concept formulated by Frisch (2006), recognizing that the generic placement of several of the species is provisional.

Key to the species of *Myriotrema* found or expected in Costa Rica (27)

1. Thallus with schizidia, isidia, or soralia 2
- Thallus lacking vegetative propagules 5

2. Thallus with soralia; psoromic acid ..... ***M. pulverulentum***
- Thallus with schizidia or isidia; chemistry variable 3

3. Thallus with cylindrical, decumbent isidia; psoromic acid ..... ***M. hartii***
- Thallus with flattened schizidia; stictic or hypoprotocetraric acid and lichexanthone 4

4. Stictic acid ..... ***M. frondosolucens***
- Hypoprotocetraric acid ..... ***M. neofrondosum***

5. Ascospores transversely septate 6
- Ascospores (sub-)muriform 20

6. No substances or medulla with yellow pigment 7
- Psoromic, olivaceic, or hypoprotocetraric acid and sometimes additionally lichexanthone 8

7. Medulla with yellow pigment; apothecia lacking columella ..... ***M. endoflavescens***
- Medulla unpigmented; apothecia often pseudocolumellate ..... ***M. album***

8. Psoromic acid 9
- Hypoprotocetraric or olivaceic acid, sometimes additionally lichexanthone 15

9. Ascospores 1-septate, 6–8 µm long; cortex loose; apothecia often elongate-aggregated ..... ***M. uniseptatum***
- Ascospores 3–7-septate, 9–24 µm long; cortex variable; apothecia not elongate or aggregated 10

10. Apothecia erumpent to prominent, 0.4–1 mm diam. 11
- Apothecia immersed, 0.2–0.4 mm diam. 13

11. Apothecia with free excipulum and distinct fenestrate pseudocolumella; ascospores 10–18 µm long ***M. costaricense***
- Apothecia with fused excipulum and irregular pseudocolumella; ascospores 15–24 µm long 12

12. Thallus sorediate; ascospores 5–7-septate ..... ***M. pulverulentum***
- Thallus lacking soralia; ascospores 3–5-septate ..... ***M. glaucophaenum***

13. Cortex loose; ascospores 9–12 µm long ..... ***M. myriotremoides***
- Cortex dense; ascospores 10–20 µm long 14

14. Apothecia with free excipulum; ascospores 10–15 µm long ..... ***M. microporum***
- Apothecia with fused excipulum; ascospores 15–20 µm long ..... ***M. clandestinum***

15. Olivaceic acid; apothecia with free excipulum ..... ***M. olivaceum***
- Hypoprotocetraric acid and often additionally lichexanthone; excipulum variable 16

16. Apothecia erumpent to prominent (at least when mature), with free excipulum, often dense and covering the entire thallus 17
- Apothecia immersed, with fused excipulum, numerous but not covering the entire thallus 19

17. Thallus with loose cortex; ascospores 10–15 µm long; lichexanthone present ..... ***M. glauculum***
- Thallus with dense, prosoplectenchymatous cortex; ascospores 15–20 µm long; lichexanthone absent 18

18. Apothecia prominent with steep margin, dense and covering the entire thallus ..... ***M. congestum***
- Apothecia at first immersed but becoming prominent with gently sloping margin, numerous but not covering the entire thallus surface ..... ***M. plurifarium***

19. Thallus with schizidia; ascospores 10–15 µm long ..... ***M. neofrondosum***
- Thallus lacking schizidia; ascospores 16–24 µm long ..... ***M. microporellum***

20. Ascospores brown; thallus minutely grainy due to columnar clusters of crystals; protocetraric acid..... ..... ***M. laeviusculum***
- Ascospores colorless; thallus smooth to uneven; no substances or psoromic, protocetraric, hypoprotocetraric, or norstictic acid 21

21. Psoromic, protocetraric, or norstictic acid 22
- Hypoprotocetraric acid or no substances 27

22. Norstictic acid ..... ***M. norsticticum***
- Psoromic or protocetraric acid 23

23. Protocetraric acid ..... ***M. thailandicum***
- Psoromic acid 24

24. Thallus with decumbent, cylindrical isidia ..... ***M. hartii***
- Thallus lacking isidia 25

25. Apothecia prominent, usually dense and covering entire thallus ..... ***M. concretum***
- Apothecia immersed, numerous but not covering entire thallus 26

26. Apothecia with distinct white rim; ascospores 15–20 × 8–10 µm, I+ distinctly violet-blue ..... ***M. classicum***
- Apothecia lacking white rim; ascospores 20–28 × 12–15 µm, I+ weakly violet-blue ..... ***M. clandestinoides***

27. No substances 28
- Hypoprotocetraric acid and often additionally lichexanthone 29

28. Apothecia porinoid, aggregate to almost pseudostromatic, with fused excipulum ..... ***M. aggregans***

- Apothecia myriotremoid, numerous but dispersed, with free excipulum ..... ***M. subconforme***
  (if apothecia myriotremoid with fused excipulum and dark margin, see *Pycnotrema pycnoporellum*)

29. Apothecia erumpent to prominent, 0.3–0.8 mm diam., often with irregular pseudocolumella ..... ***M. viridialbum***
- Apothecia immersed, 0.15–0.25 mm diam.., lacking columella ..... ***M. myrioporoides***

Myriotrema aggregans* Sipman & Lücking, *spec. nov. (Fig. 15G)
MycoBank #800078

Differing from *Myriotrema album* and *Pycnotrema pycnoporellum* in the aggregate, small apothecia resembling perithecia.

Holotype:—COSTA RICA. Guanacaste: Monte Alto Forest Reserve, Monte Alto Biological Station (Tempisque Conservation Area), Nicoya Pensinsula, 150 km W of San José, 10 km SSE of Nicoya, near Hojancha, main trails and access road through reserve near station (Sendero Jardín de Orquideas, Sendero Ceiba, Sendero Shannon-Ward); 85° 24' W, 10° 02' N, 450–550 m; lowland to lower montane moist forest zone, disturbed primary and oldgrowth secondary forest, on bark (twig), semi-exposed; Mar 2004, *Sipman 51996* (INB-0004063567; isotype: B).

Thallus light grey-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.1–0.2 mm diam., aggregate in irregular to almost pseudostromatic groups; disc covered by narrow, 0.05 mm wide pore, invisible; margin entire, brown. Columella absent. Excipulum prosoplectenchymatous, brown; periphysoids absent. Hymenium 60–70 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 5–7 transverse septa and 0–1 longitudinal septa per segment, 18–25 × 7–9 µm, ellipsoid, with thick septa and rounded lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This new species somehow resembles *Pycnotrema pycnoporellum* (see below), but differs in the very small, irregularly aggregate, almost porinoid apothecia. There is also great similarity with *Leucodecton compunctum* (see above), which is supposed to include forms with colorless or brown ascospores. It is at present unclear whether the new species could be alternatively placed in either *Leucodecton* or *Pycnotrema*; forms of *L. compunctum* with colorless ascospores are similar but have larger ascospores and the apothecia are not aggregate.

Additional specimens examined (paratypes):—COSTA RICA. Alajuela: Volcán Tenorio National Park, Pilón Biological Station (Arenal-Tempisque Conservation Area), Tilarán Ridge, 140 km NW of San José, 25 km NNW of Tilarán, near Bijagua, access road to station and river; 84° 59' W, 10° 43' N, 700 m; lower montane cloud forest zone, exposed trees and fence posts along pasture, on bark (lower trunk), exposed; Mar 2004, *Sipman 51814* (B, INB). Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, second part of trail from Los Patos to Sirena station; 83° 33' W, 8° 32' N, sea level; lowland rain forest zone, oldgrowth secondary forest and closed secondary vegetation, on bark (lower stem), semi-exposed; Apr 2003, *Sipman 51104f* (B, INB).

***Myriotrema album* Fée** (Fig. 15H)

Myriotrema album Fée, Essai Crypt. Exot.: 104 (1825); *Thelotrema myriotrema* Nyl., Mem. Soc. Sci Nat. Cherbourg 5: 107 (1857) [nom. nov.]; *Thelotrema album* (Fée) Nyl., Bull. Soc. Linn. Normand., Ser. 2(2): 74 (1868); *Ocellularia alba* (Fée) Müll. Arg., Mém. Soc. Phys. Hist. Nat. Genève 29(8): 6 (1887). Lectotype (Hale 1978: 12): 'America meridionalis', s.col. (G!).

Thallus light yellow-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.2–0.4 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, flesh-colored, white-pruinose; margin entire, fused, white. True columella absent but irregular, fenestrate pseudocolumella usually present. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3-septate, 15–20 × 5–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Myriotrema album* appears to be one of the few genuine species in the genus lacking lichen substances. Most similar is *M. myrioporum* (Tuck.) Hale, which differs in the smaller, 1-septate ascospores and the absence of a pseudocolumella. Another species lacking substances is *Myriotrema subconforme* (see below), which has a free excipulum and submuriform ascospores. *Myriotrema album* is known from a single collection already reported by Breuss (2006). It is unclear why Nylander (1857) proposed the new name *Thelotrema myriotremoides* for *Myriotrema album*, as there is no earlier homonym in *Thelotrema*.

Specimens examined:—COSTA RICA. Puntarenas: Golfito region, Bosque Esquinas, Fila trail near Esquinas Rainforest Lodge; Aug 1999, *Breuss 15795..59* (LI).

Myriotrema clandestinoides* Sipman & Lücking, *spec. nov. (Fig. 16A)
MycoBank #800079

Differing from *Myriotrema clandestinum* in the submuriform ascospores.

Holotype:—COSTA RICA. San José: Along road from San Jerónimo to Alto La Palma, N of San José; 84° 01' W, 10° 00' N, 1500 m; on fence poles and scattered trees among pasture fields and gardens; 1988, *Sipman et al. 41567* (B; isotype: CR).

Thallus light grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.2–0.4 mm diam.; disc covered by narrow, 0.07–0.15 mm wide pore, barely visible; margin entire, fused, white. Columella absent. Excipulum prosoplectenchymatous, light brown; periphysoids present, short, conglutinated. Hymenium 100–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3–5 transverse and 0–2 longitudinal septa per segment, 20–28 × 12–15 µm, ellipsoid, with thickened septa and lens-shaped lumina and thickened outer wall, colorless, I+ weakly violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This new species is placed in *Myriotrema* with much hesitation. The short periphysoids and the I+ weakly amyloid ascospores with thickened outer wall suggest placement in *Thelotrema*, but the myriotremoid apothecia with fused excipulum and the psoromic acid chemistry exclude such a placement. No currently known genus in the family has a combination of characters similar to this new taxon. Several species of *Myriotrema* agree in morphology and chemistry, but *Myriotrema* s.str. lacks periphysoids and the ascospores are I+ distinctly amyloid and have a thin outer wall. In several aspects, the new species resembles *Schizotrema cryptotrema*, except that the ascospores are much smaller and the excipulum is not layered. It is likely that this species forms a separate lineage in the *Topeliopsis* clade, which comprises taxa with very disparate morphology, including several previously placed in *Myriotrema* and *Thelotrema* (Rivas Plata & Lumbsch 2011a, b).

***Myriotrema clandestinum* (Fée) Hale** (Fig. 16B)

Myriotrema clandestinum (Fée) Hale, Mycotaxon 11: 133 (1980) [non *Pyrenula clandestina* Ach. ≡ *Clandestinotrema clandestinum* (Ach.) Rivas Plata, Frisch & Sipman]; *Thelotrema clandestinum* Fée, Mem. Soc. Mus. Hist. Nat. Strasbourg 2(2): 90 (1837). Lectotype (Hale 1974: 32): 'America', s.col. (G!).

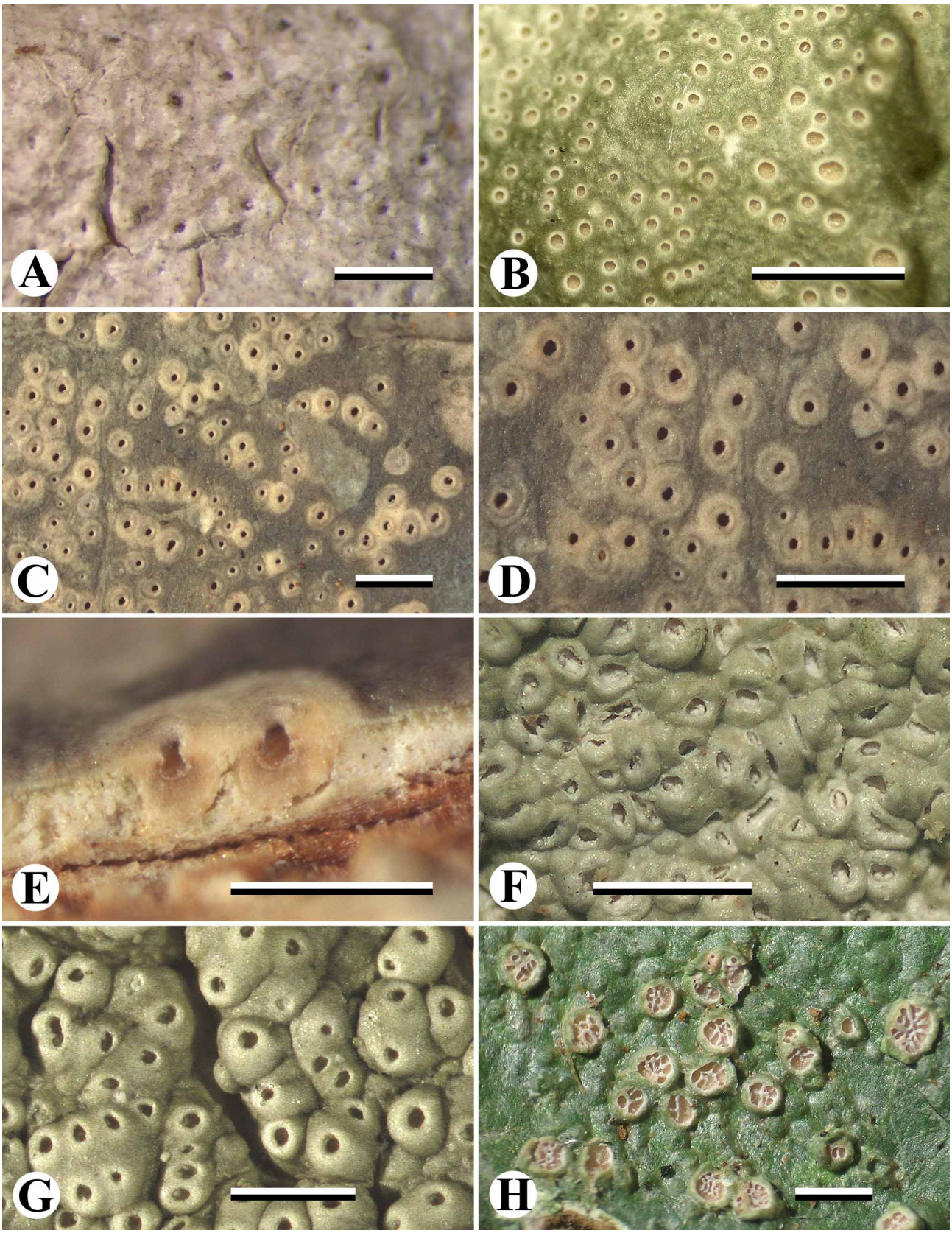

FIGURE 16. A. *Myriotrema clandestinoides*. B. *Myriotrema clandestinum*. C–E. *Myriotrema classicum*. F. *Myriotrema concretum*. G. *Myriotrema congestum*. H. *Myriotrema costaricense*. Scale = 1 mm.

Thelotrema terebratulum Nyl., Ann. Sci. Nat., Bot., Sér. 5, 7: 315 (1867); *Ocellularia terebratula* (Nyl.) Müll. Arg., Mém. Soc. Phys. Genève 29(8): 12 (1887); *Myriotrema terebratulum* (Nyl.) Hale, Mycotaxon 11: 135 (1980). Lectotype (Hale 1974: 32). Colombia, *Lindig 129* (H-NYL 22637!; isolectotypes: FH!, G!).

Thelotrema clandestinum f. *remanens* Nyl., Ann. Sci. Nat., Bot., Sér. 5, 7: 317 (1867); *Thelotrema remanens* (Nyl.) Müll. Arg., Mém. Soc. Phys. Genève 29(8): 7 (1887). Holotype. Colombia, *Lindig 90* (H-NYL!).

Thallus light grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.2–0.3 mm diam.; disc covered by narrow, 0.07–0.12 mm wide pore, invisible; margin entire, fused, yellow-white. Columella absent. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3-septate, 15–20 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This species is characterized by its myriotremoid thallus and apothecia (immersed with narrow pore), a fused excipulum, 3-septate ascospores, and psoromic acid. There are a number of other species with the same chemistry and (similar) ascospore type: *Myriotrema costaricense* and *M. glaucophaenum* (see below) have larger, prominent, partially pseudocolumellate apothecia, *M. fragile* (Hale) Hale has a verrucose-bullate thallus, *M. myriotremoides* (see below) differs by its loose cortex and smaller ascospores, *M. uniseptatum* (see below) lacks a cortex and has 1-septate, very small ascospores, *M. temperatum* Mangold has a verrucose thallus and erumpent apothecia, and *M. microporum* (Mont.) Hale has a free excipulum (double margin).

Specimens examined:—COSTA RICA. Unknown locality, *Chaves s.n.* (INB). Guanacaste: Upper portion of cañon of Río San José; 460–480 m; Feb 1930; *Dodge & Thomas 55* (FH).

Myriotrema classicum* Lücking, *spec. nov. (Fig. 16C–E)
MycoBank #800080

Differing from *Myriotrema clandestinum* in the submuriform ascospores and broad white apothecial margin.

Holotype:—COSTA RICA. Puntarenas: Monte Verde, Cordillera de Tilaran, ca. 20 km E of Juntas; Jan 1979, *Filson 16344* (MEL).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.3–0.5 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, invisible; margin entire, fused, forming a broad yellow-white rim around the pore. Columella absent. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3 transverse and 0–1 longitudinal septa per segment, 15–20 × 8–10 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This new species differs from other species with submuriform ascospores and psoromic acid chiefly in apothecial morphology: *Myriotrema concretum* and *M. hartii* (see below) have prominent to sessile apothecia lacking a white rim and the excipulum is free in the latter species, which also produces isidia. *Myriotrema rugiferum* (Harm.) Hale shares the immersed apothecia with *M. classicum* but has a free excipulum (double margin) and also lacks the white rim characteristic of the new species. Most similar in apothecial anatomy is *M. clandestinum* (see above), which has transversely septate ascospores and also lacks a broad white rim around the apothecial pore. The epithet was chosen because the apothecia of the new species resemble the whitewall tires of classic automobiles.

***Myriotrema concretum* (Fée) Hale** (Fig. 16F)

Myriotrema concretum (Fée) Hale, Mycotaxon 11: 133 (1980); *Thelotrema concretum* Fée, Essai Crypt. Exot., Suppl.: 90 (1837). Lectotype (Hale 1878: 41). 'America meridionalis', s.col. (G!; isolectotype: H-NYL!).

Thallus light grey-olive-yellow, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent to almost sessile, rounded, 0.2–0.4 mm diam.; disc partially covered by 0.2 mm wide pore, pale brown, white-pruinose; margin entire, with (indistinct) split between thallus and proper margin, yellow-white. Columella absent. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 70–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–1 longitudinal septa per segment, 12–15 × 5–7 µm, ellipsoid, with thick septa and rounded lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—*Myriotrema concretum* is one of several species with psoromic acid and small, colorless ascospores. It appears to be most closely related to *M. glaucophaenum* and relatives (*M. viridalbum* group according to Frisch 2006), but this has to be tested by molecular data. Superficially it resembles *M. congestum*, which, however, has transversely septate ascospores and hypoprotocetraric acid. The isidiate counterpart of *M. concretum* is *M. hartii* (see below).

Specimens examined:—COSTA RICA. Cartago: Chiripó National Park, trail from Base Crestones to San Gerardo; 83° 29' W, 9° 29' N, 2500 m; disturbed primary mossy mountain forest, on trunk along trail; Mar 2000, *Sipman & Umaña 46562* (B, INB). San José: Cordillera de Talamanca, 5 km W of Cerro de la Muerte, San Gerardo de Dota, along Quebrada Ojo de Agua; 83° 48' W, 9° 35' N, 2600 m; epiphyte; Mar 1985, *Sipman & Chaverri 20776* (B, CR), *20805* (B, CR). Rio Macho Forest Reserve, Villa Mills; 83° 41' W, 9° 34' N, 2750 m; primary forest, on bark; Apr 1999, *Tobler 16* (ASU).

***Myriotrema congestum* (Hale) Hale** (Fig. 16G)

Myriotrema congestum (Hale) Hale, Mycotaxon 11: 133 (1980); *Ocellularia congesta* Hale, Smithson. Contr. Bot. 38: 17 (1978). Holotype. Panama, *Hale 43470* (US!).

Thallus light grey-green, smooth to uneven, with dense, paraplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent to almost sessile, rounded, 0.2–0.4 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, invisible; margin entire, with (indistinct) split between thallus and proper margin, white. Columella absent. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3-septate, 15–20 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids.

Remarks:—This species resembles *Myriotrema concretum* morphologically, but the latter has submuriform ascospores and psoromic acid. *Myriotrema glauculum* (see below) is also very similar but has immersed to erumpent apothecia, smaller ascospores, and a loose cortex. *Myriotrema plurifarium* (Nyl.) Frisch (Frisch 2006) is very similar, but has a prosoplectenchymatous cortex with internal splitting and the apothecia are irregularly pseudocolumellate.

Specimens examined:—Not yet known from Costa Rica, but reported from Panama (Hale 1978).

***Myriotrema costaricense* (Müll. Arg.) Hale** (Fig. 16H)

Myriotrema costaricense (Müll. Arg.) Hale, Mycotaxon 11: 133 (1980); *Ocellularia costaricensis* Müll. Arg., Bull. Soc. Bot. Belgique 30: 75 (1891); *Rhabdodiscus costaricensis* (Müll. Arg.) Vain., Ann. Acad. Sci. Fenn., Ser. A 15(6):

184 (1921); *Ocellularia alba* f. *costaricensis* (Müll. Arg.) Redinger, Arkiv Bot. 28A(8): 45 (1936). Lectotype (Hale 1981: 277). Costa Rica, *Tonduz s.n.* (G!; isolectotypes: US!, W!; Pittier, Pl. Costaric. Exs. 5321).

Myriotrema quitoense Fée, Essai Crypt. Exot., Suppl.: 90 (1837). Holotype. Ecuador, s.col. (G, not seen; isotype: US!).

Thallus light grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, angular-rounded, 0.4–0.8 mm diam.; disc partially covered by 0.2–0.5 mm wide pore, flesh-colored, partly filled by white, fenestrate pseudocolumella; margin entire, with split between thallus and proper margin (double margin), white. True columella absent but excipular pseudocolumella present, irregularly fenestrate, white. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 70–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–5-septate, 10–18 × 4–6 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—*Myriotrema costaricense* is a conspicuous species due to its rather large, prominent apothecia with double margin in which the free excipulum becomes irregular-fenestrate and resembles a complex columella. The species somewhat resembles a *Thelotrema* but differs clearly in thallus cortex structure, chemistry, and the absence of periphysoids. It is most closely related to *Myriotrema glaucophaenum* (see below), with which it was synonymized by Frisch (2006), but the latter has a fused excipulum and very rarely develops a simple pseudocolumella. *Leucodecton expallescens* (see above) is another similar species, which differs in having submuriform ascospores, stictic acid, and a loose cortex.

Specimens examined:—COSTA RICA. Guanacaste: Barra Honda National Park, Barra Honda Biological Station (Tempisque Conservation Area), Barra Honda Mountains, 140 km WNW of San José, 10 km ENE of Nicoya, main trail to Terciopelo cave and Mirador; 85° 21' W, 10° 10' N, 400–500 m; lowland to lower montane moist forest zone, disturbed primary and oldgrowth secondary forest with calcareous rock outcrops, on bark (lower trunk), semi-exposed; Mar 2004, *Will-Wolf 12838a* (CR, INB, USJ, WIS). Lomas de Barbudal Biological Reserve, Lomas de Barbudal Station (Tempisque Conservation Area), Río Tempisque Bassin, 140 km WNW of San José and 20 km WSW of Bagaces, trail from station to Río Barbudal; 85° 22' W, 10° 30' N, 100 m; lowland to lower montane moist forest zone, disturbed gallery forest and forest remnants, on bark (lower trunk), semi-exposed; Mar 2003, *Nelsen 3529* (INB, WIS); ibid., fully exposed; Mar 2003, *Lücking 16112a, b* (F, INB), *16116* (F, INB, hb. Kalb); ibid., exposed; Mar 2003, *Lücking 16119a* (F), *16119b* (INB). Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, trail to beach S of station (Sendero Los Naranjos); 83° 35' W, 8° 29' N, sea level; lowland coastal rain forest zone, coastal secondary forest and closed secondary vegetation on sandy soil, on bark (lower trunk), semi-exposed; Apr 2003, *Buck 44116* (INB, NY). Old Camino Real, a few km SE of Paso Real near the Rio Grande de Térraba; 9° 29' N, 84° 09' W, 100 m; tropical rainforest; Dec 1978, *Kalb & Plöbst 33993*, *38933*, *38935* (hb. Kalb).

Myriotrema endoflavescens **Hale ex Lücking** (Fig. 17A–B)

Myriotrema endoflavescens Hale ex Lücking in Lumbsch *et al.*, Phytotaxa 18: 86 (2011). Holotype. Panama, *Hale 44859* (US!).

Thallus light yellow-olive, smooth to uneven, in parts bullate to almost gall-forming, with dense, prosoplectenchymatous cortex with internal splitting; medulla pale yellow; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.2–0.4 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, flesh-colored, white-pruinose; margin entire, fused, light yellow. Columella absent. Excipulum prosoplectenchymatous, yellow-brown; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–5-septate, 15–20 × 5–7 µm, ellipsoid, with thick septa

and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: medulla with pale yellow pigment (K+ yellow); otherwise no substances detected by TLC.

Remarks:—Mason Hale intended to describe this very characteristic species as new but never published it formally (Lumbsch *et al.* 2011). It displays a very typical *Myriotrema* morphology and appears to be most closely related to *M. album* (see above), *M. myrioporum*, and *M. subconforme* (see below). However, no *Myriotrema* species with pigmented medulla is known to date. Most species with pigmented medulla belong in *Ocellularia* s.str. (see below). In fact, there is a species with identical pigment described below, *O. flavoperforata*, which differs in its columellate apothecia and protocetraric acid. Except for the pigmented medulla, *M. endoflavescens* resembles *M. album*, which also differs by its often present irregular pseudocolumella, and *M. myrioporum* and *M. subconforme*, respectively, which differ in their either 1-septate or submuriform ascospores.

Specimens examined:—The species is thus far only known from the type material from Panama.

Myriotrema frondosolucens* Lücking, *spec. nov. (Figure. 17C)
MycoBank #800081

Differing from *Myriotrema frondosum* and *M. neofrondosum* in the presence of stictic acid and lichexanthone.

Holotype:—COSTA RICA. Puntarenas: Corcovado National Park, Los Patos Section, Los Patos Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, access trail to station and first, hilly part (5 km) of trail to Sirena; 83° 29' W, 8° 34' N, 100–300 m; lowland rain forest zone, closed primary forest, on bark (branch, fallen), exposed; Apr 2003, *Lücking 16309a* (F).

Thallus light grey-olive to pale yellow-white, smooth to uneven, producing schizidia, with loose cortex; schizidia 0.15–0.25 mm diam.; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia not observed. Secondary chemistry: stictic acid and lichexanthone.

Remarks:—This species is here described formally although apothecia are unknown, because of its unique combination of characters. The schizidia are similar to those of *Myriotrema frondosum* Hale (with psoromic acid) and *M. neofrondosum* (see below; with hypoprotocetraric acid), and these species appear to be closely related. Placement of this group of species in *Myriotrema* is provisional and almost certainly they belong to a distinct clade, but thus far no molecular data are available for any of the species.

***Myriotrema glaucophaenum* (Kremp.) Hale** (Fig. 17D)

Myriotrema glaucophaenum (Kremp.) Hale, Mycotaxon 11: 133 (1980); *Thelotrema glaucophaenum* Kremp., Nuov. Giorn. Bot. Ital. 7: 19 (1875); *Ocellularia glaucophaena* (Kremp.) Zahlbr., Cat. Lich. Univ. 2: 591 (1923). Lectotype (Hale 1978: 21). Malaysia (Borneo), *Beccari 92* (M!; isolectotype: G!).

Thelotrema emergens Vain., Ann. Acad. Sci. Fenn., Ser. A, 15(6): 192 (1921); *Ocellularia emergens* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 590 (1923). Holotype. Philippines, *Weber 1416* (TUR-VAIN 26885!; isotype: NY!).

Myriotrema subcostaricense Sipman, Acta Bot. Fenn. 150: 168 (1994). Holotype. Guyana, *Sipman & Aptroot 19424* (B!).

Thallus light grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, angular-rounded, 0.5–1 mm diam.; disc partially covered by 0.2–0.5 mm wide pore, pale brown, white-pruinose; margin entire to fissured, fused, white. Columella absent. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–5-septate, 13–24 × 5–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

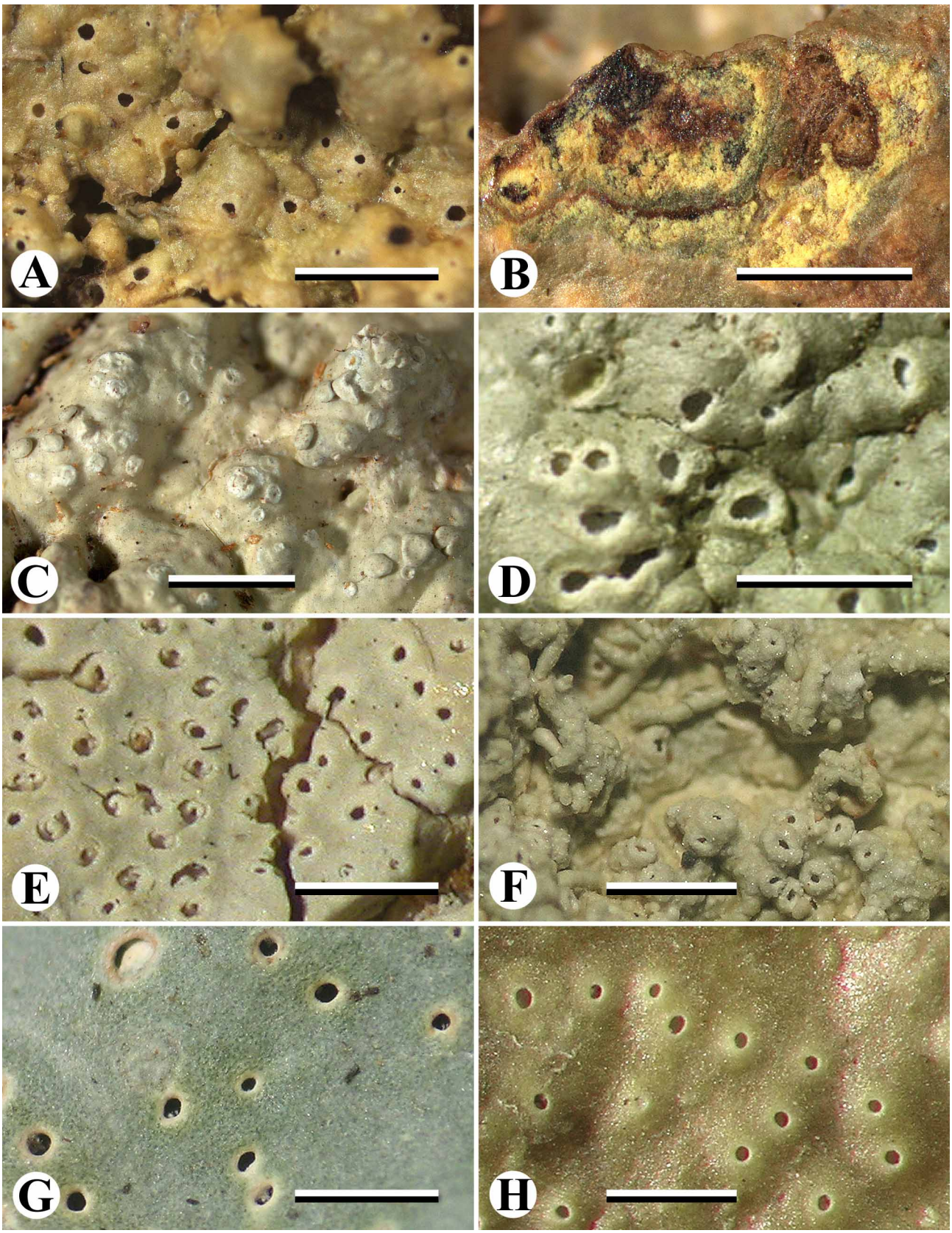

FIGURE 17. A–B. *Myriotrema endoflavescens*. C. *Myriotrema frondosolucens*. D. *Myriotrema glaucophaenum*. E. *Myriotrema glauculum*. F. *Myriotrema hartii*. G. *Myriotrema laeviusculum*. H. *Myriotrema microporellum*. Scale = 1 mm.

Remarks:—*Myriotrema glauophaenum* is characterized by *Ocellularia*-like, prominent apothecia, but otherwise agrees well with species of *Myriotrema* with immersed, myriotremoid apothecia in thallus and excipular structure and the iodine reaction of the ascospores. Molecular data suggest a close relationship with *Stegobolus* s.str. (Rivas Plata *et al.* 2012b). The similar *M. concretum* (see above) differs by its submuriform ascospores, whereas *M. costaricense* (see above) has larger apothecia with distinct, irregular to fenestrate pseudocolumella.

Specimens examined:—COSTA RICA. Guanacaste: Barra Honda National Park, Barra Honda Biological Station (Tempisque Conservation Area), Barra Honda Mountains, 140 km WNW of San José, 10 km ENE of Nicoya, main trail to Terciopelo cave and Mirador; 85° 21' W, 10° 10' N, 400–500 m; lowland to lower montane moist forest zone, disturbed primary and oldgrowth secondary forest with calcareous rock outcrops, on bark (lower trunk), semi-exposed; Mar 2004, *Aptroot 60863* (BR, INB).

***Myriotrema glauculum* (Nyl.) Hale** (Fig. 17E)

Myriotrema glauculum (Nyl.) Hale, Mycotaxon 11: 133 (1980); *Thelotrema glauculum* Nyl., Ann. Sci. Nat. Bot., Ser. 4, 19: 332 (1863). Lectotype (Hale 1978: 23). Cuba, *Wright s.n.* (H-NYL 22639!).

Thelotrema leptoporum Nyl., Mém. Soc. Sci. Nat. Cherbourg 5: 118 (1857); Nylander in Leighton, Trans. Linn. Soc. London 27: 167 (1869); *Thelotrema* '*leptosporum*' [sic] Zahlbr., Cat. Lich. Univ. 2: 594 (1923). Cuba, *Wright s.n.* (BM!; isotypes: FH!, G!,UPS!, US!).

Thallus light grey, smooth to uneven, with loose cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.1–0.2 mm diam.; disc covered by narrow, 0.07–0.15 mm wide pore, invisible; margin entire, with split between thallus and proper margin, white. Columella absent. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3-septate, 10–14 × 5–6 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids, lichexanthone.

Remarks:—*Myriotrema glauculum* is closely related to *M. congestum* (see above), but *M. congestum* differs in the dense cortex and prominent apothecia and the absence of lichexanthone. *Myriotrema uniseptatum* (see below) looks superficially similar to *M. glauculum* but has psoromic acid and 1-septate ascospores.

Specimens examined:—Not yet known from Costa Rica, but reported from Panama (Hale 1978).

***Myriotrema hartii* (Müll. Arg.) Hale** (Fig. 17F)

Myriotrema hartii (Müll. Arg.) Hale, Mycotaxon 11: 133 (1980); *Thelotrema hartii* Müll. Arg., Flora 69: 311 (1886). Lectotype (Hale 1981: 284). Jamaica, *Hart s.n.* (G!; isolectotypes: BM!, NY!).

Thelotrema insigne Zahlbr., Denkschr. Math.-Nat. Kl. K. Akad. Wiss. Wien 83: 120 (1909); *Fibrillithecis insignis* (Zahlbr.) Frisch, Biblioth. Lichenol. 92: 138 (2006). Holotype. Brazil, *Wettstein & Schiffner s.n.* (W!).

Thallus light grey-green, smooth to uneven, producing isidia, with dense, prosoplectenchymatous cortex; isidia up to 1 mm long and 0.15 mm thick, usually decumbent; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent to sessile, rounded, 0.2–0.4 mm diam.; disc partially covered by 0.1–0.2 mm wide pore, pale brown, white-pruinose; margin entire, with (indistinct) split between thallus and proper margin, white. Columella absent. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 60–70 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3 transverse septa and 0–1 longitudinal septa per segment, 10–15 × 6–10 µm, ellipsoid, with thick septa and rounded lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—*Myriotrema hartii* is one of several distantly related, myriotremoid species that produce large isidia (Rivas Plata *et al.* 2010a, 2012c). Frisch (2006) included in the newly established genus *Fibrillithecis* the isidiate *F. insignis*, but revision of the type revealed it to be conspecific with *M. hartii* and a synonym of the latter (Rivas Plata *et al.* 2010a). The isidiate *Fibrillithecis* material was subsequently described as *F. confusa* (see above), a species remarkably similar to *Myriotrema hartii* in the isidiate thallus, the prominent to sessile apothecia, the submuriform, amyloid ascospores, and the presence of psoromic acid (Rivas Plata *et al.* 2010a). However, *F. confusa* has larger apothecia with a smaller, distinctly fibrillate pore, and the isidia are thicker and always erect and often dark-tipped. Material belonging to *Myriotrema hartii* has also been found in Venezuela [*Sipman 26631* (B, VEN)] and Guyana [*Sipman & Aptroot 19087* (B, BRG)]. *Myriotrema hartii* resembles in apothecia and thallus characters closely *M. concretum* (see above), of which it can be considered the isidiate counterpart.

Specimens examined:—COSTA RICA. Alajuela: Juan Castro Blanco National Park; 84° 22' W, 10° 16' N, 1800–1900 m; Apr 2009, *Chaves 3686* (INB). Guanacaste: Volcán Tenorio National Park, Alto Masis Section (Arenal-Tilarán Conservation Area), Tilarán Ridge, 125 km NW of San José, 15 km NNW of Tilarán, near Tierras Morenas, surroundings of station; 85° 00' W, 10° 37' N, 950–1000 m; lower montane elfin cloud forest zone, disturbed low elfin forest and secondary vegetation, on wood (fence post), fully exposed; Mar 2004, *Trest 1577* (INB); ibid., on wood (fence post), exposed; Mar 2004, *Nelsen 3795* (INB, USJ, WIS). San José: San Gerardo de Dota, Finca Chacón, near entrance of Sendero La Quebrada; 83° 48' W, 9° 33' N, 2800 m, mixed, light, primary *Quercus* forest on steep slope, on trunk; Nov 1999, *Sipman 44331* (B).

***Myriotrema laeviusculum* (Nyl.) Hale** (Fig. 17G)

Myriotrema laeviusculum (Nyl.) Hale, Mycotaxon 11: 134 (1980); *Thelotrema laeviusculum* Nyl., Ann. Sci. Nat. Bot., Ser. 4, 19: 335 (1863). Lectotype (Hale 1978: 52). Cuba, *Wright 155* (FH!; isolectotypes: BM!, G!, UPS!).

Thallus light grey-olive, with minutely grainy surface, with loose cortex; photobiont layer and medulla with columnar clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.2–0.3 mm diam.; disc covered by narrow, 0.05–0.1 mm wide pore, invisible; margin entire, fused, yellow-white to brown. True columella absent but irregular pseudocolumella extending laterally from the excipulum often present. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 100–140 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–1 longitudinal septa per segment, 18–24 × 6–12 µm, ellipsoid, with thick septa and rounded lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: protocetraric and virensic acids.

Remarks:—*Myriotrema laeviusculum* is atypical in the genus due to its minutely grainy thallus with columnar clusters of crystals; as such, the epithet *laeviusculum* is clearly misleading. This type of thallus is found elsewhere in *Leptotrema*, *Leucodecton*, in the *Ocellularia bahiana* group, and in *Reimnitzia*. The prosoplectenchymatous excipulum of *Myriotrema laeviusculum* and the presence of protocetraric acid agree with *Ocellularia*, and indeed, molecular data show that the species is closely related to *Ocellularia bahiana* (Rivas Plata *et al.* 2012b). We have refrained from any formal recognition of this relationship, since the genus *Ocellularia* s.lat. is currently under study and the *O. bahiana* group will most probably end up in a separate genus (Rivas Plata *et al.*, in prep.).

Specimens examined:—COSTA RICA. Alajuela: San Ramón Forest Reserve, near house at Río Lorencito, 5 km NE of Cerro Jabonal; 84° 37' W, 10° 13' N, 1000 m; humid, mossy forest with many ferns on mountain ridge, on thin trunk in undergrowth; Nov 1988, *Sipman et al. 41966* (B, CR). Limón: Hitoy Cerere Biological Reserve, Hitoy Cerere Biological Station (La Amistad Caribe Conservation Area), Talamanca Ridge, 125 km ESE of San José, 40 km S of Limón, near Pandora, trails through forest above station (Sendero Espavel and Sendero Tepesquintle); 83° 02' W, 9° 40' N, 150–300 m; lowland to lower montane rain forest zone, partly disturbed primary forest, on bark (lower trunk), partially shaded; Mar 2004, *Sipman 51636* (B,

INB). Puntarenas: Las Tablas Protection Zone, La Neblina Section (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km ENE of San Vito near Las Mellizas, access road to fincas; 82° 45' W, 8° 55' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower trunk), partially shaded; Jun 2002, *Sipman 47896* (B, F, INB). San Vito de Coto Brus, Las Cruces Biological Station; 82° 58' W, 8° 47' N, 1200 m; on ridge beyond Río Java, on trunks and undergrowth of disturbed primary forest; Oct 2004, *Sipman 53257* (B, INB). Wilson Botanical Garden, Las Cruces Biological Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 190 km SE of San José, trail beyond botanical garden; 82° 58' W, 8° 47' N, 1200 m; montane rain forest zone, primary forest, on bark (lower trunk), partially shaded; Sep 2007, *Lücking 21038* (F), *OTS course P5-MR* (F).

***Myriotrema microporellum* (Nyl.) Hale** (Fig. 17H)

Myriotrema microporellum (Nyl.) Hale, Mycotaxon 11: 134 (1980); *Thelotrema microporellum* Nyl., Ann. Sci. Nat. Bot., Ser. 4, 19: 327 (1863). Lectotype (Hale 1978: 24). Cuba, *Wright 126* (FH!; isolectotypes: BM!, G!).
Thelotrema subterebratum Nyl., Boletim Soc. Broteriana 4: 210 (1886); Flora 69: 174 (1886); *Ocellularia subterebrata* (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 601 (1923). Holotype. São Thomé & Principe, *Moller s.n.* (H-NYL 22772!).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.2–0.3 mm diam.; disc covered by narrow, 0.04–0.08 mm wide pore, invisible; margin entire to fissured, fused, white. Columella absent. Excipulum prosoplectenchymatous, apically brown; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched, thick, apically capitate. Ascospores 8/ascus, 3-septate, 16–24 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids.

Remarks:—This species is very similar to *Myriotrema glauculum* (see above), but the latter has a loose cortex, a mostly free exciulum, smaller ascospores, and lichexanthone in addition to hypoprotocetraric acid. *Myriotrema congestum* (see above) and *M. plurifarium* (see below) differ by the prominent apothecia with free excipulum, whereas *M. neofrondosum* Sipman produces schizidia. *Myriotrema myrioporoides* and *M. viridialbum* (see below) differ from these species in having submuriform ascospores. *Myriotrema plurifarium* was synonymized with *Myriotrema microporellum* by Hale (1981) but clearly differs morphologically and is indeed closer to *M. viridialbum* and relatives (Frisch 2006).

Specimens examined:—Not yet known from Costa Rica, but reported from Panama (Hale 1978).

***Myriotrema microporum* (Mont.) Hale** (Fig. 18A)

Thelotrema microporum Mont., Ann. Sci. Nat., Bot., Sér. 3, 10: 130 (1848); *Coscinedia micropora* (Mont.) A. Massal., Atti Reale Ist. Veneto Sci. Lett. Arti, Ser. 3, 5: 256 (1860); *Ocellularia micropora* (Mont.) Müll. Arg., Flora 74: 112 (1891). Lectotype (Hale 1981: 286). Indonesia (Java), *Junghuhn s.n.* (PC!; isolectotypes: FH!, US!; Junghuhn, Lich. Javan. 143).
Thelotrema crassulum Nyl., Ann. Sci. Nat., Bot., Sér. 4, 11: 258 (1859); *Ocellularia crassula* (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 588 (1923). Lectotype (Hale 1981: 286). Mauritius, *Boivin s.n.* (PC!).
Ocellularia galactina Zahlbr., Ann. Crypt. Exot. 5: 216 (1932). Holotype. South Africa, *Van der Byl 673* (W!; isotype: US!).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.2–0.3 mm diam.; disc covered by narrow, 0.05–0.2 mm wide pore, invisible; margin entire, with split between thallus and proper margin, yellow-white. Columella absent. Excipulum prosoplectenchymatous, apically brown; periphysoids absent. Hymenium 50–70 µm high, clear; paraphyses unbranched, thick, apically capitate. Ascospores 8/

ascus, 3-septate, 10–14 × 5–6 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This species is close to *Myriotrema clandestinum* (see above) and differs chiefly in the apothecia with free excipulum (double margin), the apically brown excipulum, and the smaller ascospores. *Myriotrema myriotremoides* (see below) is also very similar but has a loose cortex and a fused excipulum.

Specimens examined:—COSTA RICA. Guanacaste: Lomas de Barbudal Biological Reserve, Lomas de Barbudal Station (Tempisque Conservation Area), Río Tempisque Bassin, 140 km WNW of San José and 20 km WSW of Bagaces, trail from station to Río Barbudal; 85° 22' W, 10° 30' N, 100 m; lowland to lower montane moist forest zone, disturbed gallery forest and forest remnants, on bark (lower stem), partially shaded; Mar 2003, *Lücking 16104* (F, INB, hb. Kalb).

***Myriotrema myrioporoides* (Müll. Arg.) Hale** (Fig. 18B)

Myriotrema myrioporoides (Müll. Arg.) Hale, Mycotaxon 11: 134 (1980); *Thelotrema myrioporoides* Müll. Arg., Bull. Soc. Bot. Belgique 32: 147 (1893). Lectotype (Hale 1978: 45). Costa Rica, *Tonduz s.n.* (G!).

Thallus light grey-green, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.2–0.3 mm diam.; disc covered by narrow, 0.1–0.15 mm wide pore, invisible; margin entire, with split between thallus and proper margin, white. Columella absent. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–1 longitudinal septa per segment, 12–16 × 7–10 µm, ellipsoid, with thick septa and rounded lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids, sometimes lichexanthone.

Remarks:—*Myriotrema myrioporoides* is one of two species in the genus with submuriform ascospores and hypoprotocetraric acid. The other species, *M. viridialbum* (see below), differs in the larger, prominent, often pseudocolumellate apothecia. *Myriotrema subconforme* (see below) does not produce lichen substances and has a yellow-brown excipulum, whereas another similar species, *M. rugiferum* (Harm.) Hale differs in having psoromic acid.

***Myriotrema myriotremoides* (Nyl.) Hale** (Fig. 18C)

Myriotrema myriotremoides (Nyl.) Hale, Mycotaxon 11: 134 (1980); *Thelotrema myriotremoides* Nyl., Ann. Sci. Nat. Bot., Ser. 4, 11: 221 (1859). Lectotype (Hale 1978: 25). Bolivia, *Weddell s.n.* (PC!).

Thelotrema opacum Vain., Acta Soc. Fauna Fl. Fenn. 7: 85 (1890); *Ocellularia opaca* Zahlbruckner, Cat. Lich. Univ. 2: 597 (1923); *Ocellularia albula* f. *opaca* (Vain.) Redinger, Arkiv Bot. 28A(8): 46 (1936). Lectotype (Hale 1978: 25). Brazil, Vainio s.n. (TUR-VAIN 26876!; isolectotypes: BM!, FH!, UPS!; Vainio, Lich. Bras. Exs. 808).

Thallus white-grey, smooth to uneven, with loose cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.3–0.4 mm diam., sometimes aggregate in lines; disc covered by narrow, 0.05–0.1 mm wide pore, invisible; margin annulate, white. Columella absent. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 50–60 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–5-septate, 9–12 × 3–5 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This species agrees with *Myriotrema clandestinum* (see above) in apothecial morphology and ascospore septation, but has a loose cortex and very small ascospores. It is very similar to *M. uniseptatum* (see below), which differs mainly in its even smaller, 1-septate ascospores and the often pseudocolumellate apothecia.

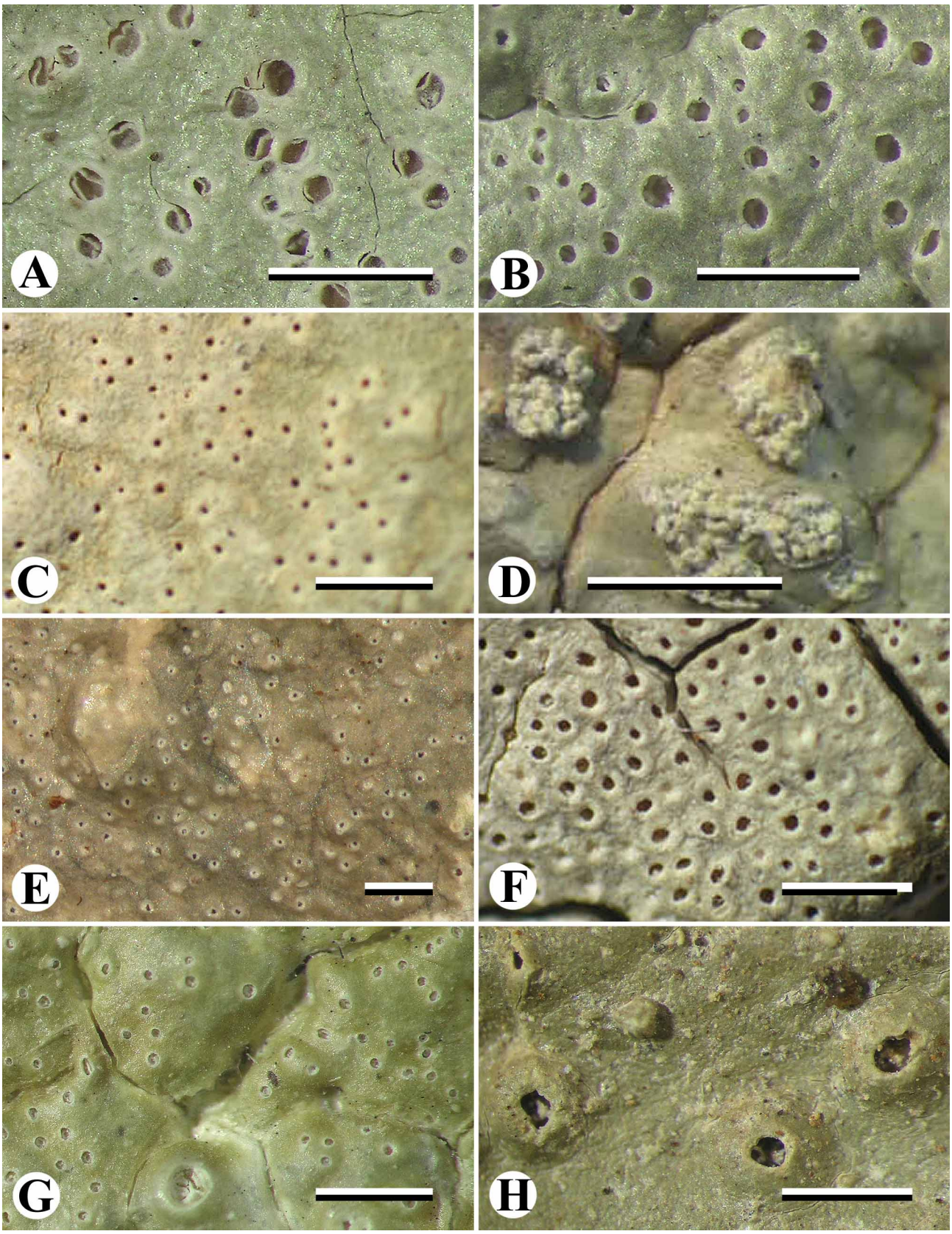

FIGURE 18. A. *Myriotrema microporum*. B. *Myriotrema myrioporoides*. C. *Myriotrema myriotremoides*. D. *Myriotrema neofrondosum*. E. *Myriotrema norsticticum*. F. *Myriotrema olivaceum*. G. *Myriotrema plurifarium*. H. *Myriotrema pulverulentum*. Scale = 1 mm.

Specimens examined:—COSTA RICA. Cartago: CATIE Agricultural Research Centre near Turrialba; 83° 40' W, 09° 55' N, 600 m; epiphytic in undergrowth of primary forest on steep slope along river, Los Espaveles trail; Nov 1988, *Sipman & Döbbeler 42378* (B, CR). Puntarenas: Finca Quebrada Bonita-Garabú, La Fila; 84° 35' W, 09° 34' N, 0–100 m; Nov 2008, *Chaves 3323*, *3326* (INB). La Amistad International Park, Altamira Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 20 km N of San Vito near Finca Colorado, trail to Casa Coca; 82° 59' W, 9° 02' N, 1800 m; montane rain forest zone, abandoned pasture with forest remnants, on bark (lower trunk), semi-exposed; Jul 2002, *Sipman 48062c*, *48063a* (B, INB).

***Myriotrema neofrondosum* Sipman** (Fig. 18D)

Myriotrema neofrondosum Sipman, Tropical Bryology 5: 85 (1992). Holotype. Guyana, *Sipman & Aptroot 18293* (B!).

Thallus light grey-green, smooth to uneven, producing schizidia, with dense, prosoplectenchymatous cortex; schizidia 0.2–0.4 mm diam., irregularly rounded and arranged in pustule-like aggregates; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.2-0.3 mm diam.; disc covered by narrow, 0.1-0.2 mm wide pore, invisible; margin entire, flesh-colored. Columella absent. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 60–70 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3-septate, 10–15 × 6–7 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids, lichexanthone.

Remarks:—This is one of three schizidiate species in *Myriotrema*, all differing chiefly in chemistry and ascospore septation (if apothecia are known). The newly described *M. frondosolucens* (see above) lacks ascomata but has stictic acid and lichexanthone, whereas *M. frondosum* Hale differs in its submuriform ascospores and psoromic acid. Except for the schizidia, *M. neofrondosum* is most similar to *M. congestum* and *M. microporellum* (see above), the latter having an apically brown excipulum and larger ascospores.

Specimens examined:—Not yet officially reported from Costa Rica but its presence was communicated by B. Emmerer (Graz).

***Myriotrema norsticticum* (Hale) Hale** (Fig. 18E)

Myriotrema norsticticum (Hale) Hale, Mycotaxon 11: 134 (1980); *Thelotrema norsticticum* Hale, Phytologia 26: 417 (1973). Holotype. Trinidad and Tobago, *Hale 37369* (US!).

Thallus light grey-green, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.2–0.3 mm diam.; disc covered by narrow, 0.1-0.2 mm wide pore, invisible; margin entire, yellow-white. Columella absent. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 60–70 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3–7 transverse septa and 0–2 longitudinal septa per segment, 12–20 × 6–10 µm, ellipsoid, with thick septa and rounded lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: norstictic acid.

Remarks:—This species is here provisionally retained in *Myriotrema* inspite of the unusual chemistry for that genus. We considered *Wirthiotrema* and *Leucodecton* as alternative homes for this taxon, but from *Wirthiotrema* it differs by the amyloid ascospores with thick septa and from *Leucodecton* by the dense, splitting cortex and prosoplectenchymatous excipulum.

Specimens examined:—Not yet known from Costa Rica but reported from Panama (Hale 1978).

***Myriotrema olivaceum* Fée** (Fig. 18F)

Myriotrema olivaceum Fée, Essai Crypt. Exot.: 103 (1825); *Ocellularia olivacea* (Nyl.) Müll. Arg., Mém. Soc. Phys. Genève 29(8): 7 (1887); *Ocellularia olivacea* (Nyl.) Overeem in Overeem-de Haas & Overeem-de Haas, Bull. Jard. Bot. Buitenzorg, sér. 3, 4: 118 (1922) [comb. superfl.]. Lectotype (Hale 1974: 24). 'South America', s.col. (G!).

Patellaria angusturae Spreng., Syst. Veget. 1: 267 (1827); nom. illeg. Lectotype (Zahlbruckner 1923: 597). 'South America', s.col. (G!).

Thelotrema subcrassulum Vain., Mycologia 21: 38 (1929); *Ocellularia subcrassula* (Vain.) Zahlbr., Cat. Lich. Univ. 8: 245 (1932). Lectotype (Hale 1974: 26). Puerto Rico, *Fink 725* (MICH!; isolectotype: US!).

Thallus pale grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.2–0.3 mm diam.; disc covered by narrow, 0.05–0.2 mm wide pore, invisible; margin entire, with split between thallus and proper margin (double margin), white. Columella absent. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3-septate, 9–13 × 5–6 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: olivaceic, *O*-methyl-olivaceic, norsubnotatic and norisonotatic acids.

Remarks:—*Myriotrema olivaceum* is the type species of the genus, which thus far only comprises this species and *M. microporum* (see above) with certainty, as confirmed by molecular data. Both species have identical thallus and apothecial morphology (double margin) but differ in chemistry (psoromic acid in *M. microporum*). The chemistry of *M. olivaceum* is indeed rather unusual and more commonly found in *Ocellularia* s.lat. It is possible that *Myriotrema* s.str. will only comprise a few species and most other species currently included in the genus will have to be reassigned. Sprengel (1827: 267) intended to describe *Patellaria angusturae* as a new species ("... *ad corticem Angusturae* ..."), but then included both *Myriotrema olivaceum* and *M. album* as synonyms. Therefore, the name *Patellaria angusturae* is illegitimate and automatically typified by the type of *M. olivaceum*, since Zahlbruckner (1923: 597) made that lectotypification.

Specimens examined:—COSTA RICA. Limón: Caribbean coast, S of Cahuita; 82° 50' W, 9° 44' N, sea level; *Cocos* trunks in orchard immediately S of the town; Jan 1979, *Sipman 12238* (U).

***Myriotrema plurifarium* (Nyl.) Frisch** (Fig. 18G)

Myriotrema plurifarium (Nyl.) Frisch, Biblioth. Lichenol. 92: 167 (2006). *Thelotrema plurifarium* Nyl., Ann. Sci. Nat. Bot., Ser. 5, 7: 315 (1867); *Ocellularia plurifaria* (Nyl.) Müller Arg. in Durand & Pittier, Bull. Soc. Bot. Belg. 30: 75 (1891). Holotype. Cuba, *Wright s.n.* (H-NYL 22631!).

Thallus light grey-olive-yellow, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia at first immersed, rounded but eventually becoming prominent, angular-rounded, 0.3–0.5 mm diam.; disc partially covered by 0.1–0.3 mm wide pore, flesh-colored, partly filled by white pseudocolumella; margin entire, with split between thallus and proper margin, yellow-white; proper margin fissured. Pseudocolumella present, fenestrate, white. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 70–80 µm high, clear; paraphyses unbranched, apically capitate. Ascospores 8/ascus, 3-septate, 10–20 × 6–9 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids.

Remarks:—This species was reported from Costa Rica by Müller (1891) but we have not been able to locate the material. *Myriotrema plurifarium* is very close to *M. glauculum* and *M. microporellum*, both with the same chemistry and ascospore type. It differs from *M. glauculum* in the irregular pseudocolumella and the dense cortex and from *M. microporellum* in the pseudocolumella and split between excipulum and thalline

margin. Like *M. viridialbum*, the apothecia of *M. plurifarium* start out immersed and myriotremoid and remain so for a long time but eventually become larger and prominent. The main difference between the two species are the submuriform ascospores in *M. viridialbum*.

Specimens examined:—Reported by Müller (1891) from Costa Rica.

***Myriotrema pulverulentum* (Hale) Hale** (Fig. 18H)

Myriotrema pulverulentum (Hale) Hale, Mycotaxon 11: 135 (1980); *Ocellularia pulverulenta* Hale, Smithson. Contr. Bot. 38: 29 (1978). Holotype. Panama, *Hale 43468* (US!).

Thallus light grey-green, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting, sorediate; soralia appearing as irregular, dispersed granules on the thallus surface, pale green; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.4–1 mm diam.; disc partially covered by 0.2–0.5 mm wide pore, flesh-colored, partly filled by white pseudocolumella; margin entire, fused, yellowish white. True columella absent but irregular pseudocolumella often present, white. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 60–70 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–7-septate, 18–24 × 6–10 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This species is here retained in *Myriotrema* with some hesitation, as it appears to be related to species in *Ocellularia* with uncarbonized excipulum, such as *O. psorbarroensis* (see below), but also shows resemblance with *Myriotrema glaucophaenum* (see above). In this group of species, *M. pulverulentum* is the only one that produces soralia.

Specimens examined:—Not yet known from Costa Rica, but reported from Panama (Hale 1978).

***Myriotrema subconforme* (Nyl.) Hale** (Fig. 19A)

Myriotrema subconforme (Nyl.) Hale, Mycotaxon 11: 135 (1980); *Thelotrema subconforme* Nyl., J. Linn. Soc., London 20: 53 (1883). Lectotype (Hale 1981: 294). Malaya, *Maingay 64* (BM!; isolectotypes: H-NYL 22587!, FH!, G!).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed, angular-rounded, 0.1–0.2 mm diam.; disc covered by narrow, 0.05–0.1 mm wide pore, invisible; margin entire, yellow-white, proper excipulum free (double margin), fissured. Columella absent. Excipulum prosoplectenchymatous, pale yellow-brown; periphysoids absent. Hymenium 60–70 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–2 longitudinal septa per segment, 10–20 × 6–9 µm, ellipsoid, with thick septa and rounded lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Myriotrema subconforme* is the only *Myriotrema* with submuriform ascospores and lacking lichen substances. Morphologically, it comes close to *M. olivaceum* and *M. microporum* (see above), but these species differ chemically and in the transversely septate ascospores. A species with similar thallus and apothecia, as well as submuriform ascospores, is *M. rugiferum* (Harm.) Hale, which produces psoromic acid.

Specimen examined:—Costa Rica. Limón: Palm swamp between Río Reventazón and Río Parismina on Castilla Farm; 20 m; Apr 1930; *Dodge & Nevermann 7406* (FH; as *Thelotrema myrioporoides* Müll. Arg.).

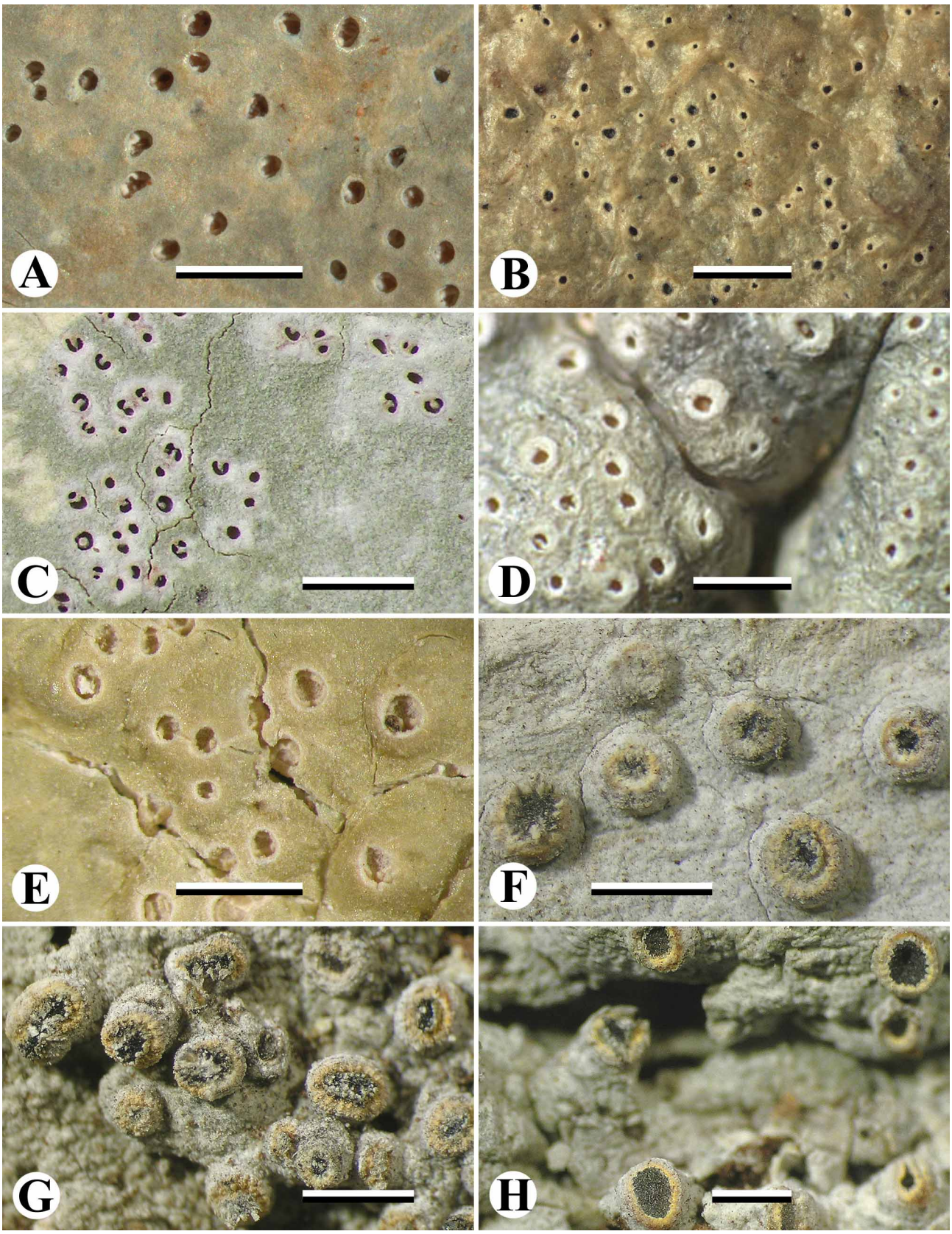

FIGURE 19. A. *Myriotrema subconforme*. B. *Myriotrema thailandicum*. C. *Myriotrema uniseptatum*. D–E. *Myriotrema viridialbum*. F–H. *Nadvornikia hawaiiensis*. Scale = 1 mm.

***Myriotrema thailandicum* Homchantara & Coppins** (Fig. 19B)

Myriotrema thailandicum Homchantara & Coppins, Lichenologist 34: 118 (2002). Holotype. Thailand, *Mongkolsuk et al. 8748* (RAMK!; isotype: E!).

Thallus grey-green, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed-erumpent, rounded, 0.2–0.4(–0.5) mm diam.; disc covered by narrow, 0.05–0.1 mm wide pore, invisible; margin entire, fused, white. Columella absent. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 5–7 transverse and 0–2 longitudinal septa per segment, 20–35 × 8–12 µm, ellipsoid, with thick septa and lens-shaped lumina, grey-brown, I+ violet-blue (amyloid) when young. Secondary chemistry: fumarprotocetraric and protocetraric acid.

Remarks:—This species is very characteristic due to the combination of grey-brown, submuriform ascospores and fumarprotocetraric and protocetraric acid. The only other species with similar ascospores and chemistry is *Myriotrema laeviusculum* (see above), in which the ascospores are dark brown and smaller, protocetraric acid is the major compound, and the thallus is minutely grainy due to the formation of columnar clusters of calcium oxalate crystals.

Specimen examined:—COSTA RICA. Puntarenas: Monte Verde, Cordillera de Tilaran, ca. 20 km E of Juntas; Jan 1979, *Filson 16379* (MEL).

***Myriotrema uniseptatum* (Hale) Hale** (Fig. 19C)

Myriotrema uniseptatum (Hale) Hale, Mycotaxon 11: 135 (1980); *Ocellularia uniseptata* Hale, Smithson. Contr. Bot. 38: 33 (1978). Holotype. Panama, *Hale 38671* (US!).

Thallus light grey, smooth to uneven, with loose cortex or partially ecorticate; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed, angular to elongate, aggregate, 0.1–0.3 mm diam.; disc covered by narrow, 0.05–0.07 mm wide pore, flesh-colored, partly filled by white pseudocolumella; margin entire, yellow-white. True columella absent but irregular pseudocolumella often present, white. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 45–55 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 1-septate, 6–8 × 3–4 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic, 2'-*O*-demethylpsoromic, and stictic acids.

Remarks:—*Myriotrema uniseptatum* is quite a distinctive species due to the loosely corticate thallus with small, often irregular or aggregate, pseudocolumellate apothecia and 1-septate ascospores. The chemistry of psoromic and stictic acid is also unusual, otherwise only known from *Myriotrema mammillare* (Hale) Hale and *Ocellularia gerardii* (see below).

Specimens examined:—Not yet known from Costa Rica, but reported from Panama (Hale 1978).

***Myriotrema viridialbum* (Kremp.) Hale** (Fig. 19D–E)

Myriotrema viridialbum (Kremp.) Hale, Mycotaxon 11: 135 (1980); *Thelotrema viridialbum* Kremp., Flora 59: 221 (1876); Hale, Smithson. Contr. Bot. 38: 12 (1978). Lectotype (Hale 1978: 12). Brazil, *Glaziou 3193* (M!; isolectotype: C!).

Thelotrema steyermarkii Hale, Phytologia 27: 496 (1974); *Myriotrema steyermarkii* (Hale) Hale, Mycotaxon 11: 135 (1980). Holotype. Venezuela, *Steyermark 98008* (US!).

Thelotrema leucohymenium Zahlbr., Denkschr. Math.-Nat. Kl. K. Akad. Wiss. Wien 83: 120 (1909). Holotype. Brazil, *Schiffner s.n.* (W!; isotype: BM!).

Thallus light grey-olive-yellow, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent to prominent, angular-rounded, 0.3–0.8 mm diam.; disc partially covered by 0.2–0.6 mm wide pore, flesh-colored, partly filled by white pseudocolumella; margin entire, with (indistinct) split between thallus and proper margin, yellow-white; proper margin fissured. Pseudocolumella present, fenestrate, white. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched, apically capitate. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–2 longitudinal septa per segment, 10–20 × 6–12 µm, ellipsoid, with thick septa and rounded lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids and satellites, lichexanthone.

Remarks:—*Myriotrema viridialbum* is one of four species of *Myriotrema* producing lichexanthone in addition to hypoprotocetraric acid and satellites substances, suggesting a close relationship. Among these, *M. viridialbum* is clearly set apart by the comparatively large, erumpent to prominent, often pseudocolumellate apothecia with free excipulum (double margin) and submuriform ascospores. *Myriotrema myrioporoides* (see above) differs chiefly in the small, immersed apothecia, but does not appear to represent a juvenile form of *M. viridialbum*. *Myriotrema glauculum* (see above) has a loosely corticate thallus, smaller apothecia, and transversely septate ascospores, whereas *M. neofrondosum* (see above) has a fused excipulum, transversely septate ascospores, and produces schizidia. *Myriotrema viridialbum* also resembles species in the *M. costaricense-glaucophaenum* complex (see above), which differ in producing psoromic acid.

Specimens examined:—COSTA RICA. Alajuela: Volcán Tenorio National Park, Pilón Biological Station (Arenal-Tempisque Conservation Area), Tilarán Ridge, 140 km NW of San José, 25 km NNW of Tilarán, near Bijagua, access road to station and river; 84° 59' W, 10° 43' N, 700 m; lower montane cloud forest zone, exposed trees and fence posts along pasture, on bark (lower trunk), exposed; Mar 2004, *Sipman 51792* (B, INB). Limón: Caribbean coast, S of Cahuita; 82° 50' W, 9° 44' N, sea level; *Cocos* trunks in orchard immediately S of the town; Jan 1979, *Sipman 12256* (B, U).

Nadvornikia Tibell

Nadvornikia Tibell, Beih. Nova Hedwigia 79: 672 (1984). Type. *Nadvornikia hawaiiensis* (Tuck.) Tibell.

Thallus white-grey, smooth to uneven, with loose cortex or in part ecorticate; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent to sessile, rounded, mazaediate; disc exposed, appearing black and powdery due to mass of accumulating ascospores; margin entire to fissured, fused to partially free apically, covered by thalline layer. Columella absent. Excipulum paraplectenchymatous, colorless to orange-brown; periphysoids absent. Paraphyses unbranched. Ascospores accumulating above asci, 1-septate, small, ellipsoid, with thick septa and walls, dark brown, I–. Secondary chemistry: stictic acid and satellite substances.

Remarks:—The genus *Nadvornikia* is easily recognized by the *Thelotrema*-like apothecia with mazaediate disc. The other distinctly mazaediate genus in the family, *Schistophoron* Stirt., differs in the slit-like disc resembling a species of *Carbacanthographis*, and is closely related to *Glyphis*. *Nadvornikia* forms part of a well-supported clade including *Wirthiotrema* and several other, non-mazaediate species with *Thelotrema*-like apothecia, such as *Myriotrema peninsulae* (Rivas Plata & Lumbsch 2011a; Rivas Plata *et al.* 2012a).

Nadvornikia hawaiiensis (Tuck.) Tibell (Fig. 19F–H)

Nadvornikia hawaiiensis (Tuck.) Tibell, Beih. Nova Hedwigia 79: 672 (1984); *Acolium hawaiense* Tuck., Proc. Amer. Acad. Arts Sci. 7: 232 (1866). Lectotype (Mangold *et al.* 2009: 655). U.S.A. (Hawaii), *Mann s.n.* (UPS!).

Tylophoron diplotylium Nyl., Bull. Soc. Linn. Normandie, Sér. 2, 2: 46 (1868); *Nadvornikia diplotylia* (Nyl.) Pant & Awasthi, Biovigyanam 15: 12 (1989). Holotype. New Caledonia, s.col. (H-NYL 40422!).

Thallus white-grey, smooth to uneven, with loose cortex or in part ecorticate; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent to sessile, rounded, mazaediate, 0.8–1.5 mm diam.; disc exposed, appearing black and powdery due to mass of accumulating ascospores; margin entire to fissured (then appearing coronate), fused to partially free apically, brown, covered by thalline layer. Columella absent. Excipulum paraplectenchymatous, colorless to orange-brown; periphysoids absent. Hymenium 80–100 µm high, disintegrating; paraphyses unbranched. Ascospores originally 8/ascus but soon expelled and accumulating above asci, 1-septate, ellipsoid, 6–10 × 4–6 µm, with thick septa and walls, dark brown, I–. Secondary chemistry: stictic, constictic, hypostictic, α-acetylconstictic, and hypoconstictic acid acids.

Remarks:—Like other mazaediate taxa, *Nadvornikia hawaiiensis* appears to be found typically on exposed trees with aged bark, preferably at mid elevations.

Specimens examined:—COSTA RICA. Puntarenas: Las Tablas Protection Zone (Amistad Pacifico Conservation Area), La Neblina section, 25 km ENE of San Vito near Las Mellizas, access road to fincas; 8° 55' N, 82° 45' W, 1600 m; montane rain forest zone: disturbed primary forest, on bark (lower trunk); Jun 2002, *Sipman 47897* (B, INB). Upper portion of cañon of Río San José; 460–480 m; Feb 1930; *Dodge & Thomas 7826* (FH; as *Phaeotrema* sp.).

Ocellularia G. Mey.

Ocellularia G. Mey., Nebenst. Beschaeft. Pflanzenk. 1: 327 (1825) [nom. cons]. Type. *O. obturata* (Ach.) Spreng. [= *O. cavata* (Ach.) Müll. Arg.].

Thallus usually grey-olive, smooth to uneven or verrucose to rarely bullate, usually with dense, proso- or paraplectenchymatous cortex; medulla often pigmented; photobiont layer and medulla (if developed) usually with clusters of calcium oxalate crystals. Apothecia (immersed-)erumpent to prominent, rounded to angular-rounded; disc (partially) covered by narrow or wider pore, often filled by columella; margin usually entire, laterally covered by thalline layer. Columella often present, usually simple, usually carbonized, often white-pruinose. Excipulum prosoplectenchymatous, brown to usually carbonized; periphysoids absent. Paraphyses unbranched but laterally anastomosing in some species. Ascospores transversely septate to muriform, small to very large, ellipsoid-fusiform to oblong-cylindrical, with thick septa and lens-shaped lumina (except in richly muriform ascospores), colorless or rarely brown, I+ violet-blue (amyloid). Secondary chemistry: variable, frequently psoromic acid or protocetraric acid or relatives and satellite substances or cinchonarum unknown, often together with pigments.

Remarks:—The genus *Ocellularia* was for a long time used to accomodate all species with transversely septate, colorless ascospores (Müller 1887b; Zahlbruckner 1923; Hale 1974, 1978). Hale (1980) redefined the genus to include all taxa with prosoplectenchymatous, carbonized excipulum lacking periphysoids. Kalb (2004) was the first in proposing smaller segregates when delimiting the genus *Ampliotrema* (validated in Frisch 2006). Frisch & Kalb (2006) again revised the generic concept, segregating from *Ocellularia* s.lat. the species with complex columella or excipular structures in the genera *Gyrotrema*, *Melanotrema*, *Redingeria*, and *Stegobolus*. This subdivision was not accepted by Mangold *et al.* (2009), due to apparent lack of support in phylogenetic studies. Indeed, *Stegobolus* was already considered polyphyletic by Frisch *et al.* (2006b). The *Ocellularia* clade is currently under further revision using a large scale molecular phylogeny (Rivas Plata *et al.* 2012b), and preliminary results suggest that the clade also includes lineages previously assigned to *Myriotrema* s.lat. (Hale 1980). All in all, *Ocellularia* s.lat. and *Myriotrema* s.lat., together comprising over 300 accepted species, will probably end up subdivided into about 10–15 genera (Rivas Plata *et al.* 2012b).

Awaiting the results of this study, at this point we have adopted a provisional concept, but contrary to Mangold *et al.* (2009) we refrain from including all current segregates in *Ocellularia* s.lat. Therefore, we have retained all species in *Ocellularia* that conform to the concept of the genus given by Frisch (2006) and Frisch & Kalb (2006). Alltogether, 53 species of *Ocellularia* sensu Frisch (2006) have been found in Costa Rica and adjacent areas of Central America.

Key to the species of *Ocellularia* found or expected in Costa Rica (59)

1. Ascospores transversely septate 2
- Ascospores (sub-)muriform 45

2. Ascospores small, 10–50 × 5–12 µm, 5–11(–13)-septate, 8/ascus 3
- Ascospores medium-sized to large, 50–270 × 10–40 µm long (11–)15–39-septate 32

3. Columella or pseudocolumella absent 4
- Columella or pseudocolumella present 11

4. Apothecial margin fissured and concentrically layered; cinchonarum unknown 5
- Apothecial margin entire; chemistry different 6

5. Medulla orange; excipulum carbonized ..... ***O. crocea***
- Medulla unpigmented; excipulum uncarbonized ..... ***O. decolorata***

6. No substances; excipulum uncarbonized ..... ***O. albocincta***
- Protocetraric or psoromic acid, sometimes additionally stictic acid; excipulum variable 7

7. Protocetraric acid; excipulum uncarbonized ..... ***O. vezdana***
- Psoromic acid; excipulum variable 8

8. Excipulum uncarbonized, colorless 9
- Excipulum carbonized 10

9. Stictic acid in addition to psoromic acid; thallus light olive; apothecia with 0.1–0.3 mm wide pore ..... ***O. gerardii***
- Psoromic acid only; thallus white-grey; apothecia with 0.1 mm wide pore ..... ***O. zamorana***

10. Ascospores 15–20 × 6–8 µm ..... ***O. calvescens***
- Ascospores 25–35 × 8–12 µm ..... ***O. umbilicata***

11. Medulla pale yellow or orange 12
- Medulla unpigmented 13

12. Ascospores 25–50 × 7–12 µm; apothecia prominent, 0.6–1 mm diam., excipulum carbonized; medulla pale yellow to pale orange, cinchonarum unknown ..... ***O. cavata***
- Ascospores 20–25 × 6–9 µm; apothecia erumpent, 0.3–0.5 mm diam., excipulum red-brown; medulla pale yellow, protocetraric acid ..... ***O. flavoperforata***

13. No substances or viridis unknown 14
- Protocetraric or psoromic acid 20

14. Apothecia immersed to erumpent, ascospores 20–35 µm long; columella simple 15
- Apothecia (erumpent to) prominent to sessile; ascospores 10–20 µm long; columella simple to irregular 17

15. Excipulum and columella both dark brown ..... ***O. papillata***
- Excipulum pale to dark brown or apically carbonized, columella carbonized 16

16. Columella apically white-pruinose; excipulum pale brown to brown; thallus olive-grey ..... ***O. laeviusculoides***
- Columella apically black; excipulum dark brown to apically carbonized; thallus yellow-grey .... ***O. subpyrenuloides***

17. Apothecia sessile; excipulum carbonized but columella colorless; ascospores 10–15 µm long; viridis unknown ..... ***O. viridis***
- Apothecia erumpent to prominent; excipulum and columella either both carbonized or both uncarbonized; ascospores 15–20 µm long; no substances 18

18. Excipulum and columella uncarbonized, columella irregular ..... ***O. barroensis***
- Excipulum and columella carbonized, columella simple 19

19. Apothecial margin black in inner parts, fissured ..... ***O. landronii***
- Apothecial margin yellow-white in inner parts, entire ..... ***O. ascidioidea***

20. Protocetraric acid 21
- Psoromic acid 26

21. Hymenium inspersed ..... ***O. inspersula***
- Hymenium clear 22

22. Apothecia prominent, 0.5–2 mm diam., with wider pore; columella irregular 23
- Apothecia erumpent, 0.3–0.8 mm diam., with narrow pore; columella simple 24

23. Ascospores 35–45 µm long ..... ***O. cryptica***
- Ascospores 15–25 µm long ..... ***O. mauritiana***

24. Columella distinctly carbonized, excipulum brown ..... ***O. violacea***
- Columella and excipulum pale to apically dark brown 25

25. Columella and excipulum pale brown, columella often absent; ascospores 15–25 µm long ..... ***O. vezdana***
- Columella and excipulum apically dark brown, columella always present; ascospores 20–40 µm long ... ***O. perforata***

26. Ascospores 30–50 µm long, 7–13-septate; excipulum pale brown but columella apically carbonized ..... ***O. pluriporoides***
- Ascospores 10–30 µm long, 3–9-septate; if columella carbonized then also excipulum carbonized 27

27. Columella and excipulum distinctly carbonized 28
- Columella and excipulum colorless to (apically dark) brown 29

28. Thallus and apothecia white-grey, sharply contrasting with the black tip of the columella visible through the pore; thallus distinctly verrucose; apothecia prominent; ascospores 15–25 µm long ..... ***O. antillensis***
- Thallus and apothecia light olive, the tip of the columella usually white-pruinose; thallus smooth to uneven or rarely finely verrucose; apothecia erumpent; ascospores 20–30 µm long ..... ***O. terebrata***

29. Apothecia 0.3–0.5 mm diam., erumpent; columella simple 30
- Apothecia 0.7–1.2 mm diam., prominent; columella irregular 31

30. Columella apically dark brown ..... ***O. minutula***
- Columella colorless ..... ***O. pseudopyrenuloides***

31. Thallus white-grey, bullate; apothecia irregular, annulate ..... ***O. albobullata***
- Thallus olive, smooth to uneven; apothecia round, not annulate ..... ***O. psorbarroensis***

32. Medulla pigmented (pale yellow, cinnabar-red, dark red or pink) 33
- Medulla unpigmented 39

33. Columella present 34
- Columella absent 36

34. Medulla pink; ascospores 7–12 µm broad; apothecia sessile ..... ***O. supergracilis***
- Medulla pale yellow or cinnabar-red; ascospores 12–25 µm broad; apothecia prominent 35

35. Medulla pale yellow ..... ***O. fecunda***
- Medulla cinnabar-red ..... ***O. cocosensis***

36. Ascospores becoming brown; medulla pink mottled with dark red ..... ***O. isohypocrellina***
- Ascospores remaining colorless; medulla orange, cinnabar-red, or pink 37

37. Medulla pink; hypoprotocetraric acid; ascospores up to 270 × 40 µm ..... ***O. rhodostroma***
- Medulla orange or cinnabar-red; no substances; ascospores up to 200 25 µm 38

38. Medulla cinnabar-red (K+ dark red); excipulum carbonized in upper half ..... ***O. mordenii***
- Medulla orange (K–); excipulum laterally carbonized ..... ***O. xanthostroma***

39. Excipulum brown; ascospores 50–100 µm long; stictic acid; columella absent ..... ***O. bullata***
- Excipulum carbonized; ascospores 50–250 µm long; chemistry variable but lacking stictic acid; columella present or absent 40

40. Psoromic acid 41
- Chemistry variable but lacking psoromic acid 43

41. Thallus with scattered, globose isidia; columella absent; ascospores 30–50 µm broad ..... ***O. globifera***
Thallus lacking isidia; columella present; ascospores 10–15 µm broad 42

42. Ascospores 50–70 µm long; thallus uneven, with prosoplectenchymatous cortex ..... ***O. tacarcunae***
- Ascospores 80–200 µm long; thallus verrucose, with paraplectenchymatous cortex ..... ***O. ripleyi***

43. Ascospores 10–12 µm broad, more than 10 times as long as broad; cortex prosoplectenchymatous; cinchonarum unknown; columella present ..... ***O. rhabdospora***
- Ascospores 20–40 µm broad, less than 10 times as long as broad; cortex paraplectenchymatous; hypoprotocetraric acid or no substances; columella present or absent 44

44. No substances; columella present ..... ***O. dolichotata***
- Hypoprotocetraric acid; columella usually absent or present in few apothecia ..... ***O. domingensis***

45. Ascospores small, 15–40 × 10–16 µm 46
- Ascospores medium-sized to large, 60–700 × 20–55 µm 52

46. Hymenium inspersed; excipulum brown; psoromic acid ..... ***O. inspersata***
- Hymenium clear; excipulum brown or carbonized; chemistry variable 47

47. Ascospores (dark) brown; excipulum brown 48
- Ascospores colorless; excipulum carbonized 51

48. No substances ..... ***O. urceolaris***
- Protocetraric acid 49

49. Thallus surface smooth; section with scattered crystal clusters; ascospores fusiform ..... ***O. laevigatula***
- Thallus surface minutely grainy; section with columnar crystal clusters; ascospores ellipsoid 50

50. (Pseudo-)columella present, well-developed ..... ***O. obturascens***
- (Pseudo-)columella absent or present in few apothecia and then usually rudimentary ..... ***O. bahiana***

51. Columella present ..... ***O. conformis***
- Columella absent ..... ***O. subcarassensis***

52. Columella absent; hypoprotocetraric often present 53
- Columella present; hypoprotocetraric acid absent 56

53. Ascospores submuriform, becoming brown; medulla pink mottled with dark red (section K+ aeruginous to yellow-green) ..... ***O. isohypocrellina***
- Ascospores richly muriform, colorless or brown; medulla pale yellow or unpigmented (section K+ orange-red) ... 54

54. Medulla with pale yellow pigment; thallus verrucose-bullate; excipulum laterally carbonized ..... ***O. aurulenta***
- Medulla unpigmented; thallus smooth to verrucose; excipulum brown to apically dark brown..... 55

55. Ascospores colorless; excipulum orange-brown; apothecia erumpent; psoromic acid ..... ***O. inturgescens***
- Ascospores becoming brown; excipulum apically dark brown; apothecia prominent; hypoprotocetraric acid..... ***O. chiriquiensis***

56. Stictic acid; ascospores 300– 700 µm long..... ***O. subpraestans***
- Other substances; ascospores 80–300 µm long 57

57. No substances; ascospores becoming brown, up to 100 µm long ..... ***O. terrabensis***
- Psoromic, subpsoromic, or protocetraric acids; ascospores remaining hyaline, usually exceeding 100 µm and up to 280 µm long 58

58. Psoromic acid..... 59
- Protocetraric or subpsoromic acid 60

59. Thallus smooth, with prosoplectenchymatous cortex, light olive; apothecia annulate; columella carbonized in upper half ..... ***O. maxima***
- Thallus verrucose, with paraplectenchymatous cortex, light yellow-olive; apothecia not annulate; columella entirely carbonized ..... ***O. interposita***

60. Ascospores 80–120 µm long; protocetraric acid ..... ***O. praestantoides***
- Ascospores 100–280 µm long; subpsoromic acid ..... ***O. praestans***

Ocellularia albobullata **Lücking, Sipman & Grube** (Fig. 20A)

Ocellularia albobullata Lücking, Sipman & Grube in Lumbsch *et al.*, Phytotaxa 18: 87 (2011). Holotype. Costa Rica,, *Grube 11580* (INB-4066756!; isotype: GZU!).

Thallus white-grey, bullate, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, angular-rounded to irregular, 0.7–1.2 mm diam.; disc covered by narrow, 0.2–0.3 mm wide pore, filled by brown, white-pruinose pseudocolumella; margin annulate, white, laterally covered by thick thalline layer. Pseudocolumella present, irregular, brown, white-pruinose. Excipulum prosoplectenchymatous, orange-brown; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–5-septate, 10–20 × 6–9 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This new species is easily recognized by its irregularly bullate thallus with white-grey color. It belongs to a small number of *Ocellularia* species with psoromic acid in which the thallus does not have the characteristic olive-green color but is more or less white. Other such species include *O. antillensis* (see below) and the Australian *O. wirthii* Mangold, Elix & Lumbsch (Mangold *et al.* 2008c, 2009) which, among other characters, are separated from *O. albobullata* by their non-bullate thallus and carbonized excipulum. *Ocellularia calvescens* is similar to *O. albobullata* in chemistry and ascospores but has a non-bullate thallus, lacks a columella, and has a carbonized excipulum. *Ocellularia albobullata* appears to be a lowland coastal species.

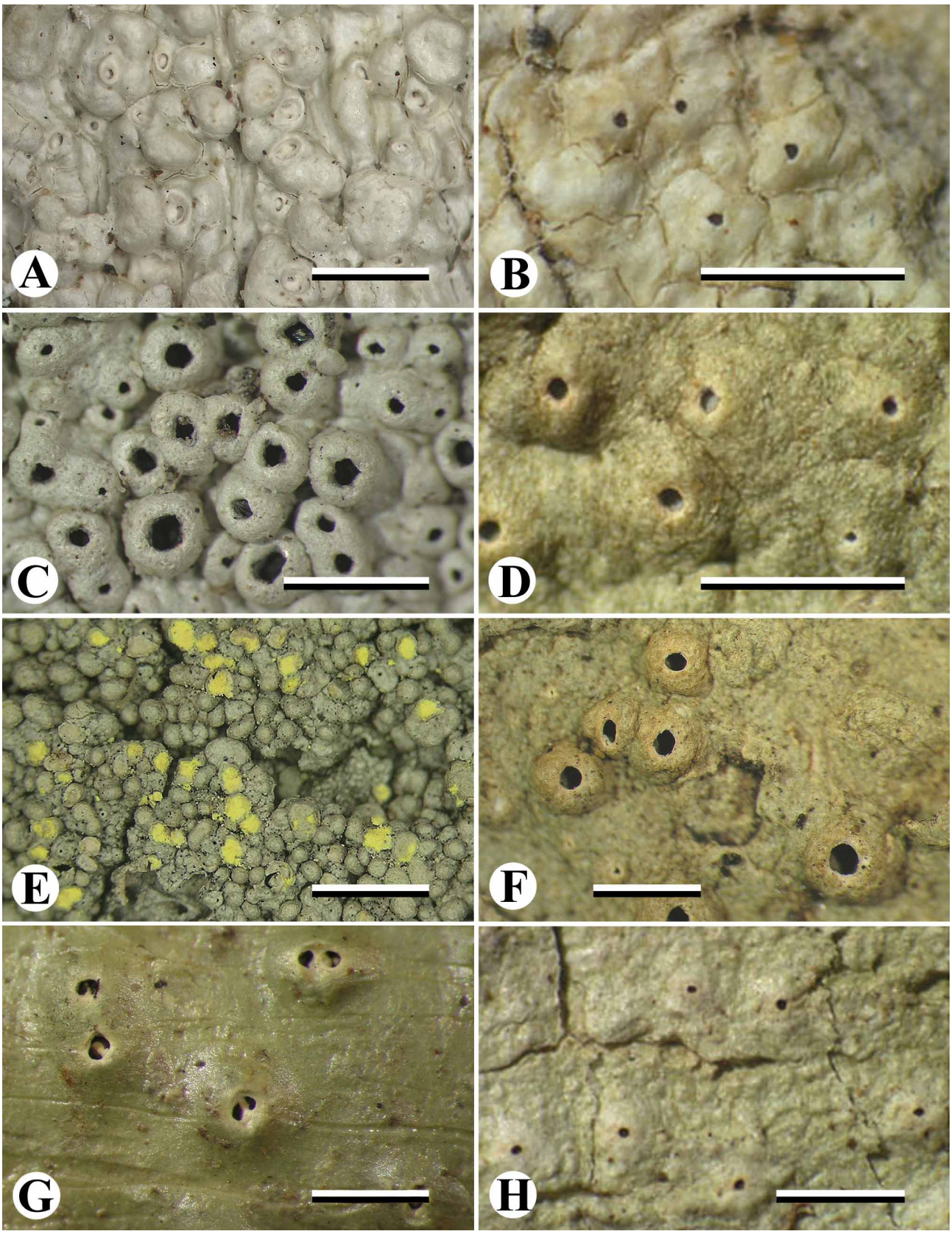

FIGURE 20. A. *Ocellularia albobullata*. B. *Ocellularia albocincta*. C. *Ocellularia antillensis*. D. *Ocellularia ascidioidea*. E. *Ocellularia aurulenta*. F. *Ocellularia bahiana*. G. *Ocellularia barroensis*. H. *Ocellularia calvescens*. Scale = 1 mm.

Additional specimens examined (paratypes):—COSTA RICA. Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, beach south of station; 83° 36' W, 8° 28' N, sea level; lowland coastal rain forest zone, disturbed coastal forest and exposed trees along beach, on bark (lower stem), semi-exposed; Apr 2003, *Sipman 51123* (B, INB).

Ocellularia albocincta (Hale) Divakar & Mangold (Fig. 21B)

Ocellularia albocincta (Hale) Divakar & Mangold, Lichenologist 42: 135 (2010); *Myriotrema albocinctum* Hale, Bull. Brit. Mus. (Nat. Hist.), Bot., Ser. 8: 273 (1981). Lectotype (here selected). Sri Lanka, *Hale 46331* (US!).

Thallus light grey-olive, uneven-verrucose and often cracked, with dense, prosoplectenchymatous cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.3–0.5 mm diam.; disc covered by 0.05–0.1 mm wide pore, flesh-colored; margin entire, yellow-white, laterally covered by thalline layer. Columella absent. Excipulum prosoplectenchymatous, pale brown; periphysoids absent. Hymenium 80–110 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–7-septate, 15–30 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This is the only species of *Ocellularia* with an uncarbonized excipulum that lacks a columella and secondary substances and has small, transversely septate, colorless ascospores. In spite of the uncarbonized excipulum, the apothecial anatomy and morphology suggests close relationship with *O. papillata* and related species, rather than *Myriotrema* s.str. *Ocellularia papillata* chiefly differs in the dark brown excipulum and columella, whereas *O. barroensis* has prominent apothecia with irregular pseudocolumella. The most similar species is *O. rhicnoporoides* Homchantara & Coppins, which has an apically carbonized excipulum (Papong *et al.* 2010). The type material of *Myriotrema albocinctum* contains discordant pieces representing two different species, one with uncarbonized and one with apically carbonized excipulum, the latter corresponding to *O. rhicnoporoides*. We have therefore selected a piece with uncarbonized apothecia (already annotated by T. Matsumoto in 1996) as lectotype. The two collections cited below are remarkable for their ecological divergence: one is from an upper montane cloud forest at nearly 3000 m altitude, whereas the other is from lowland rain forest at sea level. Both collections agree in all important details, although *Sipman 46553* has larger, more abundant crystals in the thallus.

Specimens examined:—COSTA RICA. Cartago: Chiripó National Park, trail from Base Crestones to San Gerardo; 83° 29' W, 9° 29' N, 2950 m; disturbed primary mossy mountain forest, on trunk along trail; Mar 2000, *Sipman & Umaña 46553* (B, INB). Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, second part of trail from Los Patos to Sirena station; 83° 33' W, 8° 32' N, sea level; lowland rain forest zone, oldgrowth secondary forest and dense secondary vegetation, on bark (lower stem), semi-exposed; Apr 2003, *Sipman 51088d* (B, INB).

Ocellularia antillensis Hale (Fig. 20C)

Ocellularia antillensis Hale, Smithson. Contr. Bot. 16: 17 (1974). Holotype. Lesser Antilles (Dominica), *Hale 35612* (US!).

Thallus white-grey, verrucose, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.3–0.6 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, filled by black columella; margin entire, white, laterally covered by thick

thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–7-septate, 15–25 × 7–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—*Ocellularia antillensis* is a very characteristic species due to the white thallus with numerous apothecia in which the black tip of the columella is seen through the pore. The combination of psoromic acid and white thallus is rare among *Ocellularia* species. Otherwise it somewhat resembles *Stegobolus granulosus* (see below), which differs chiefly in the olive-green thallus and broader columella. In Costa Rica, the species appears to be coastal in distribution and was mostly found in the southern Pacific parts, close to Panama, from which it was reported by Hale (1978). The collection from montane rain forest (*Kalb & Plöbst 31698*) has a more yellowish thallus and is akin towards Stegobolus granulosos; its identification is tentative.

Specimens examined:—COSTA RICA. Cartago: Cordillera de Talamanca, Interamerican Highway, 11 km S of Cartago; 83° 55' W, 9° 48' N, 1650 m; lower montane rain forest; Dec 1978, *Kalb & Plöbst 31698* (hb. Kalb). Limón: Caribbean coast S of Cahuita; sea level; *Cocos* treetrunks in orchard immediately S of the town; Jan 1979, *Sipman 12294* (B). Gandoca-Manzanillo Wildlife Refuge, Manzanillo Section (La Amistad Caribe Conservation Area), Manzanillo, 170 km ESE of San José, 65 km SE of Limón, trail along beach; 82° 53' W, 9° 38' N, sea level; lowland coastal moist forest zone, disturbed coastal vegetation with *Cocos nucifera*, *Coccoloba uvifera*, and *Rhizophora mangle*, on bark (lower trunk) of *Cocos nucifera*, exposed; Mar 2004, *Sipman 51699* (B, INB). Puntarenas: Puntarenas: Corcovado National Park, Los Patos Section, Los Patos Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, access trail to station and first, hilly part (5 km) of trail to Sirena; 83° 29' W, 8° 34' N, 100–300 m; lowland rain forest zone, closed primary forest, on bark (lower trunk), semi-exposed; Apr 2003, *Nelsen 3567g* (INB, WIS). Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay, 150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), partially shaded; Feb 1997, *Lücking 97-106a* (F), *97-108b* (F, CR, USJ), *97-153* (F, CR, USJ).

***Ocellularia ascidioidea* Hale** (Fig. 20D)

Ocellularia ascidioidea Hale, Bull. Brit. Mus. Nat. Hist., Bot. Ser., 8: 300 (1981). Holotype. Sri Lanka, *Hale 47035* (US!; isotype: BM!).

Thallus light grey-olive, minutely verrucose, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with columnar clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.6–0.9 mm diam.; disc partially covered by 0.2–0.5 mm wide pore, grey; margin entire, yellow-white, laterally covered by thalline layer. Columella absent. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 100–150 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–7-septate, 15–20 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ brown-violet (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This species belongs in a difficult group of taxa with small, colorless, transversely septate ascospores. It is characterized by its lack of secondary substances and the comparatively large, prominent apothecia. Most similar are *O. barroensis* and *O. landronii* (see below); the first differs in the uncarbonized excipulum and columella and the second in the black columella and proper margin and the often fissured thalline margin. Hale (1981) compared the species to *O. papillata* (see below), but that species has smaller, erumpent apothecia and a brown excipulum and columella.

Specimens examined:—COSTA RICA. Guanacaste: Palo Verde National Park, Palo Verde Station (Tempisque Conservation Area), Río Tempisque Bassin, 130 km WNW of San José and 30 km SSW of Bagaces, lower parts of Guayacan trail; 85° 21' W, 10° 21' N, 10–50 m; lowland to lower montane moist forest

zone, disturbed primary forest remnants and open secondary forest, on bark (lower stem), semi-exposed; Mar 2003, *Sipman 50984* (INB, B).

***Ocellularia aurulenta* Hale** (Fig. 20E)

Ocellularia aurulenta Hale, Phytologia 27: 490 (1974). Holotype. Panama, *Hale 38548* (US!).

Thallus light grey-green, verrucose-bullate, with dense, paraplectenchymatous cortex; medulla pale yellow; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.3–0.6 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, invisible; margin entire, white-grey, laterally covered by partly eroding thalline layer. Columella absent. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 250–300 µm high, clear; paraphyses unbranched. Ascospores 1–2/ascus, richly muriform, 150–200 × 25–35 µm, ellipsoid, with slightly thickened septa and rectangular lumina, colorless, I+ violet (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids, medulla with yellow (K+ red) pigment.

Remarks:—This species is the only representative among *Ocellularia* with large, muriform ascospores that has a pigmented medulla. It is easily recognized in the sterile state due to the verrucose-bullate thallus that exposes the pale yellow medulla when the verrucae break open. This lowland rain forest species was reported from Panama (Hale 1978) and has also been found in adjacent areas of southern Costa Rica.

Specimens examined:—COSTA RICA. Puntarenas: Garabito, Jaco, Finca Quebrada Bonita-Garabú, La Fila (Pacifico Central Conservation Area); 84° 35' W, 9° 34' N, 0–100 m; secondary forest, on bark (lower trunk), semi-exposed; Nov 2008, *Chaves 3284* (INB).

***Ocellularia bahiana* (Ach.) Frisch** (Fig. 20F)

Ocellularia bahiana (Ach.) Frisch, Biblioth. Lichenol. 92: 503 (2006); *Thelotrema lepadinum* var. *bahianum* Ach., Meth. Lich.: 132 (1803); *Thelotrema bahianum* (Ach.) Ach., Kgl. Vetensk. Akad. Nya Handl. 33: 87 (1812); *Leptotrema bahianum* (Ach.) Müll. Arg., Mém. Soc. Phys. Hist. Nat. Genéve 29(8): 12 (1887); *Myriotrema bahianum* (Ach.) Hale, Mycotaxon 11: 132 (1980). Lectotype (Hale 1972: 192; Frisch & Kalb 2006: 504). Brazil, s.col. (H-ACH 743!; left specimen on the sheet; isolectotype: H-NYL 22460b!).

Thelotrema develatum Nyl., Acta Soc. Sci. Fenn. 7: 454 (1863); *Leptotrema develatum* (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 633 (1923). Lectotype (Hale 1978: 50). Colombia, *Lindig 774* (BM!; isolectotypes: FH!, H-NYL 22456!, M!, PC!, W!).

Ocellularia rudius var. *dominicanum* Vain., Ann. Acad. Sci. Fenn., Ser. A 6(7): 136 (1915); *Leptotrema rudius* var. *dominicanum* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 639 (1923). Holotype. Lesser Antilles (Dominica), *Elliott 1303* (TUR-VAIN 26768!).

Thallus grey-olive-yellow, minutely grainy, with loose cortex; photobiont layer and medulla with columnar clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.4–1 mm diam.; disc partially covered by 0.2–0.6 mm wide pore, brown-black, thinly white-pruinose; margin entire, brown, laterally covered by thick thalline layer. Columella absent but rudimentary pseudocolumella sometimes present in few apothecia. Excipulum prosoplectenchymatous, apically brown; periphysoids absent. Hymenium 100–150 µm high, clear; paraphyses unbranched, thick. Ascospores 8/ascus, muriform, 17–35 × 10–15 µm, ellipsoid, with thick septa and rounded lumina, brown, young I+ violet (amyloid). Secondary chemistry: protocetraric and virensic acids.

Remarks:—*Ocellularia bahiana* belongs to a group of species that possibly deserves generic status (Rivas Plata *et al.* 2012b). The thallus is usually minutely grainy due to columnar clusters of calcium oxalate crystals, ascospores are usually brown, and the protocetraric acid chemosyndrome is present. The group also includes *Ocellularia obturascens* (see below), *O. bonplandii* Spreng., *Myriotrema erodens* Harris, and *M.*

laeviusculum (see above), among other species. The species of this group are reminescent of *Leptotrema* and *Leucodecton* in thallus structure and ascospore type but are not related to these genera (Rivas Plata *et al.* 2012b). *Ocellularia bahiana* is a greatly misunderstood species. According to various authors, it includes species with and without columella and with wide or narrow pore (Redinger 1936; Salisbury 1972b; Harris 1995; Frisch & Kalb 2006; Mangold *et al.* 2009). We have studied a large number of specimens from northeastern Brazil (Cáceres 2007), which includes the type locality, and they mostly have prominent apothecia with a wide pore and lacking a columella; a rudimentary pseudocolumella can sometimes be seen in a few apothecia. On the other hand, specimens from Florida (Harris 1995) always have a distinct and regular columella, whereas those from Australia (Mangold *et al.* 2009) all have a narrow pore and lack a columella. We are convinced that different taxa are involved here and thus restrict *O. bahiana* to material with wide pore usually lacking a columella, whereas the distinctly (pseudo-)columellate forms are named *O. obturascens* (see below; Mangold *et al.* 2009). *Ocellularia bahiana* s.str. is remarkably similar to *Ampliotrema* in general morphology and chemistry, but can be distinguished by the columnar thallus crystals, the uncarbonized, apically brown excipulum, the non-inspersed hymenium, and the dark brown ascospores. Most similar to *O. bahiana* is *O. urceolaris* (see below), which differs in the absence of lichen substances. *Ocellularia bahiana* was reported from Costa Rica by Müller (1893) as *Leptotrema bahianum*. It appears to have a broad ecological amplitude but is mostly found at higher elevations or in humid forests close to the coast exposed to mist.

Specimens examined:—COSTA RICA. Alajuela: San Ramón Forest Reserve, near station at Río Lorencito, 5 km NE of Cerro Jabonal; 84° 37' W, 10° 13' N, 1000 m; humid, mossy forest with many ferns on mountain ridge, on thin trunk in undergrowth; Nov 1988, *Sipman et al. 41959* (B, CR), *41978* (B, CR). Cartago: Cerros de la Carpintera Protection Zone, Finca La Peregrina; 83° 59' W, 09° 53' N, 1800–1900 m; Aug 2008, *Chaves 3185* (INB). Limón: Caribbean coast, S of Cahuita; 82° 49' W, 9° 44' N, sea level; on *Cocos* trunks in orchard 4 km E of the town; Jan 1979, *Sipman 12270* (U). Puntarenas: La Amistad International Park, Altamira Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 20 km N of San Vito near Finca Colorado, interpretative trail (Sendero Gigantes) behind station; 83° 00' W, 9° 02' N, 1500–1600 m; montane rain forest zone, disturbed primary forest and secondary vegetation dominated by *Cecropia*, on bark (lower stem), partially shaded; Jun 2002, *Lücking 15213* (F, INB), *15217b* (F, INB), *Sipman 48012* (B, INB), *48032f* (B, INB); ibid., trail to Casa Coca; 83° 00' W, 9° 02' N, 1600–1800 m; montane rain forest zone, secondary forest and open secondary vegetation dominated by *Cecropia*, on bark (lower trunk), partially shaded; Jul 2002, *Lücking 15264d* (INB); ibid., trail to Casa Coca; 82° 59' W, 9° 02' N, 1800 m; montane rain forest zone, primary forest remnant, on bark (lower trunk), fully shaded; Jul 2002, *Sipman 48053* (B, INB), *48056* (B, INB); ibid., semi-exposed; Jul 2002, *Sipman 48064* (B, INB); ibid., trail from Casa Coca to Valle del Silencio; 82° 59' W, 9° 02' N, 1800–1900 m; montane rain forest zone, primary oak forest, on bark (lower trunk), fully shaded; Jul 2002, *Sipman 48066a* (B, INB), *48066b* (B, INB). Near Las Cruces Botanical Garden (Coto Brus), 4 km SSE of San Vito; 82° 57' W, 8° 43' N, 1300 m; premontane rain forest zone, shady montane rain forest on slope near waterfall of Rio Jaba, on trunk; Jan 1979, *Sipman 11984* (U). Las Tablas Protection Zone, Cedro Ridge, Las Alturas Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km NE of San Vito near Alturas, surroundings of station and trail into forest; 82° 50' W, 8° 57' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower trunk), partially shaded; Jun 2002, *Lücking 15065a* (F, USJ); ibid., on bark (stem base), fully shaded; Jun 2002, *Lücking 15075* (F, INB); ibid., on bark (lower stem), partially shaded; Jun 2002, *Lücking 15076e* (F), *15076f* (INB); ibid., pasture with group of trees bordering forest, on bark (lower trunk); Jun 2002, *Sipman 47818e* (B, INB). Las Tablas Protection Zone, La Neblina Section (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km ENE of San Vito near Las Mellizas, access road to fincas; 82° 45' W, 8° 55' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower trunk), partially shaded; Jun 2002, *Sipman 47894* (B, INB), *47895* (B, INB). Upper portion of cañon of Río San José; 460–480 m; Feb 1930; *Dodge & Thomas 7826* (FH; as *Leptotrema wightii*). San José: Vicinity of El General; 850 m; on tree by river; Jan 1936; *Skutch 2394* (FH; as *Leptotrema develatum* (Nyl.) Zahlbr.).

***Ocellularia barroensis* Hale** (Fig. 20G)

Ocellularia barroensis Hale, Smithson. Contr. Bot. 38: 14 (1978); *Myriotrema barroense* (Hale) Hale, Mycotaxon 11: 132 (1980). Holotype. Panama, *Hale 46069* (US!).

Thallus light grey-olive, smooth to uneven or rarely verrucose, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.6–0.9 mm diam.; disc partially covered by 0.2–0.5 mm wide pore, flesh-colored, partially filled by white pseudocolumella; margin entire, yellow-white, laterally covered by thalline layer. Pseudocolumella present, irregular, white. Excipulum prosoplectenchymatous, brown; periphysoids absent. Hymenium 100–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–7-septate, 15–23 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Ocellularia barroensis* anatomically and chemically resembles *O. papillata* (see below), but the latter has smaller, immersed-erumpent apothecia with a more or less carbonized, true columella. Also similar and probably closely related is *O. landronii* (see below), which has a carbonized, true columella and a carbonized excipulum. *Ocellularia mauritiana* (see below) agrees with *O. barroensis* in morphology, including the uncarbonized, irregular columella and uncarbonized excipulum, but produces protocetraric acid. *Ocellularia barroensis* is a lowland rain forest species. The collection from Wilson Botanical Garden has a verrucose thallus.

Specimens examined:—COSTA RICA. Puntarenas: Carara Biological Reserve, 15 km SSW of Orotina; 84° 37' W, 9° 47' N, 50 m; disturbed primary forest, along trail near warden's house, on fallen tree; Nov 1988, *Sipman & Döbbeler 42236* (B, CR), *42241* (B, CR). Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, round trail NW of station (Sendero Sirena and Sendero Guanacaste); 83° 35' W, 8° 29' N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (lower stem), partially shaded; Apr 2003, *Lücking 16202d* (INB), *Lücking 16203* (F, INB); ibid., second part of trail from Los Patos to Sirena station; 83° 33' W, 8° 32' N, sea level; lowland rain forest zone, oldgrowth secondary forest and closed secondary vegetation, on bark (lower stem), semi-exposed; Apr 2003, *Sipman 51103c* (B, INB). Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay, 150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), fully shaded; Feb 1997, *Lücking 97-178* (F), *97-250* (F, CR, USJ). Wilson Botanical Garden, Las Cruces Biological Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 190 km SE of San José, trail beyond botanical garden; 82° 58' W, 8° 47' N, 1200 m; montane rain forest zone, primary forest, on bark (lower trunk), fully shaded; Sep 2007, *Hernandez s.n.* (F).

***Ocellularia bullata* Hale**

Ocellularia bullata Hale, Smithson. Contr. Bot. 38: 15 (1978). Holotype. Panama, *Hale 38478* (US!).

Thallus grey-green, verrucose-bullate, producing isidia; isidia up to 0.3 mm long and 0.1 mm thick, slightly clavate; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.4–0.5 mm diam.; disc covered by narrow, 0.1–0.15 mm wide pore, invisible; margin entire, pale brown, laterally covered by thalline layer. Columella absent. Excipulum prosoplectenchymatous, apically brown; periphysoids absent. Hymenium 100–150 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 9–19-septate, 50–100 × 9–18 µm, oblong, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: stictic and constictic acids.

Remarks:—This species is quite unusual in *Ocellularia* due to its chemistry and most probably does not belong in *Ocellularia* or *Myriotrema* s.str. However, at present we do not see any alternative in generic placement. The species appears to be unrelated to *Leucodecton* and *Wirthiotrema*, in which most stictic acid-containing myriotremoid species are now placed.

Specimens examined: *Ocellularia bullata* is not yet known from Costa Rica, but was reported from Panama (Hale 1978).

***Ocellularia calvescens* (Fée) Müll. Arg.** (Fig. 20H)

Ocellularia calvescens (Fée) Müll. Arg., Mém. Soc. Phys. Hist. Nat. Genève 29(8): 8 (1887); *Thelotrema calvescens* Fée, Essai Crypt. Exot.: 89 (1825); *Myriotrema calvescens* (Fée) Hale, Mycotaxon 11: 132 (1980). Lectotype (Hale 1978: 15). 'America', s.col. (G!; isolectotype: H!).

Ocellularia sexlocularis Zahlbr. in Magnusson & Zahlbruckner, Arkiv Bot. 31A: 48 (1943). Holotype. U.S.A. (Hawaii), *Faurie 678* (W!; isotype: BM!).

Thallus light grey-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.5–0.8 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, invisible; margin annulate, white, laterally covered by thalline layer. Columella absent. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 100–150 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–7-septate, 15–25 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—*Ocellularia calvescens* belongs in the *O. papillata* group and within that group shares the chemistry and ascospore type with *O. terebrata* (see below). The latter differs in the presence of a (carbonized) columella. Mangold *et al.* (2009) synonymized *Thelotrema calvescens* and *Ocellularia sexlocularis* under *O. terebrata*, assuming variability in the formation of columella structures from absent to irregular to present. In the Costa Rican material, we have not observed such variation and the non-columellate forms are easily separated from the columellate forms. We therefore retain *O. calvescens* as separate taxon. Most similar is *O. umbilicata*, which chiefly differs in its larger ascospores. The specimen *Sipman 48391a* deviates by its dull thallus and large (1.0 mm diam.) fruit warts with wide pore showing the disc. *Ocellularia calvescens* was found at mid elevations.

Specimens examined:—COSTA RICA. Guanacaste: Monte Alto Forest Reserve, Monte Alto Biological Station (Tempisque Conservation Area), Nicoya Pensinsula, 150 km W of San José, 10 km SSE of Nicoya, near Hojancha, main trails and access road through reserve near station (Sendero Jardín de Orquideas, Sendero Ceiba, Sendero Shannon-Ward); 85° 24' W, 10° 02' N, 450–550 m; lowland to lower montane moist forest zone, disturbed primary and oldgrowth secondary forest, on bark (lower trunk), exposed; Mar 2004, *Sipman 51984* (B, INB), *52015* (B, INB). Puntarenas: Fila Cruces Ridge, surroundings of Las Cruces Tropical Botanical Garden, 4 km SSE of San Vito; 8° 43' N, 82° 58' W, 1550 m; in a premontane rainforest at a waterfall; Jan 1979, *Kalb & Plöbst 32017* (hb. Kalb). Las Cruces Biological Station, San Vito de Coto Brus; 82° 58' W, 8° 47' N, 1200 m; on ridge beyond Río Java, on trunks and undergrowth of disturbed primary forest; Oct 2004, *Sipman 53269* (B, INBio). Monteverde, Cordillera de Tilaran, near the cheese factory; 84° 49' W, 10° 18' N, 1450 m; premontane rain forest zone, forest relicts among pasturefields, on trunks; Jan 1979, *Sipman 12101* (U), *12120* (U), *12122* (U).

***Ocellularia cavata* (Ach.) Müll. Arg.** (Fig. 21A)

Ocellularia cavata (Ach.) Müll. Arg., Flora 64: 499 (1882); *Thelotrema cavatum* Ach., Kongl. Vetensk. Akad. Nya Handl. 33: 92 (1812). Lectotype (Hale 1974: 17). Sierra Leone, *Afzelius s.n.* (H-ACH 750!; isolectotypes: S!, UPS!).

Thelotrema obturatum Ach., Nova Acta Reg. Acad. Sci. Holmiae 33: 92 (1812); *Ocellularia obturata* (Ach.) Spreng., Linn. Syst. Veg., Edit. 16, 4(1): 242 (1827); *Thelotrema cavatum* var. *obturatum* (Ach.) Nyl., Mém. Soc. Sci. Nat. Cherbourg 5: 118 (1858); *Ocellularia cavata* var. *obturata* (Ach.) Redinger, Ark. Bot. 28A(8): 39 (1936). Lectotype (Hale 1972: 197; Frisch 2006: 207). Sierra Leone, *Afzelius s.n.* (H-ACH 752!; isolectotypes: BM!, H-NYL 22816!, UPS!).

Ascidium cinchonarum Fée, Méth. Lichénogr. Gen.: Tab. 1, fig. 22 (1824) ('1825'); Essai Crypt. Exot.: 96 (1825); *Ocellularia cinchonarum* (Fée) Spreng., Linn. Syst. Veget., Edit. 16, 4(1): 242 (1827); *Thelotrema cinchonarum* (Fée) Vain., Étud. Lich. Brésil 2: 82 (1890). Lectotype (Hale 1974: 17). 'South America', s.col. (G!; isolectotypes: H-NYL 22390!, L!, M!, PC!).

Ascidium cinchonarum f. *intermedium* Nyl., Ann. Sci. Nat., Bot., Sèr. 5, 7: 319 (1867). Holotype. Colombia, *Lindig s.n.* (H-NYL 22385!; isotypes: BM!, G!).

Thelotrema inscalpens Nyl., Ann. Sci. Nat. Bot., Sér. 5, 7: 319 (1867). Lectotype (Mangold *et al.* 2009: 655). Colombia, *Lindig 41* (H-NYL 22558!).

Ocellularia lindigiana Müll. Arg., Mèm. Soc. Phys. Hist. Nat. Gèneve 29(8): 9 (1887); *Thelotrema lindigianum* (Müll. Arg.) Harm., Bull. Séanc. Soc. Sci. Nancy, Sér. 3, 13: 48 (1912). Lectotype (Hale 1974: 17). Colombia, *Lindig 2757* (G!; isolectotype: FH!).

Ascidium xanthostromizum Nyl., Sert. Lich. Trop. Labuan Singapore: 20 (1891); *Ocellularia xanthostromiza* (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 604 (1923). Holotype. Singapore, *Almquist s.n.* (H!).

Thelotrema chrysostroma Vain., Ann. Acad. Sci. Fenn., Ser. A, 15(6): 187 (1921). Holotype. Malaysia (Borneo), *Moulton s.n.* (TUR-VAIN 26872!; isotype: NY!).

Thallus grey-olive, smooth to uneven, with dense, paraplectenchymatous cortex; medulla pale orange; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.6–1 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, filled by brown-black columella; margin entire, black, laterally covered by often eroding thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 100–150 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–15-septate, 25–70 × 7–12 µm, oblong, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: cinchonarum unknowns, medulla with pale orange (K+ red) pigment.

Remarks:—*Ocellularia cavata* is the generic type of *Ocellularia*. This and related species have a pigmented medulla, often in combination with cinchonarum unknown or other rare secondary substances, rather conspicuous, prominent apothecia with well-developed columella, medium-sized to large, mostly transversely septate ascospores, and a more or less paraplectenchymatous cortex (Rivas Plata *et al.* 2012b). In many species the apothecial margin erodes to expose the pigmented medulla. Since this phenomenon is most commonly observed in this group, one might assume a functional role of exposing the pigment to potential dispersal agents such as ants. *Ocellularia cavata* has an extensive synonymy (Hale 1974, 1978; Frisch 2006; Mangold *et al.* 2009) and the circumscription of this species is somewhat unclear. The synonyms listed here are those where conspecifity with the type of *Thelotrema cavatum* has been definitely established by us.

Specimens examined:—COSTA RICA. Alajuela: Cerros de Mondongo de San Ramón; 750–800 m; Jan 1930; *Brenes 9* (FH; as *Ocellularia cinchonarum* var. *verrucosa* (Fée) Müll. Arg.). Cartago: Tapantí National Park, Tapantí Section, Tapantí Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 35 km SE of San José and 18 km SE of Cartago, road above second trail to river (Sendero La Pava) below Mirador; 83° 47' W, 9° 44' N, 1700 m; montane cloud forest zone, primary forest margin along roadside, on bark (lower trunk), semi-exposed; Apr 2003, *Buck 44145* (INB, NY). Puntarenas: Las Tablas Protection Zone, Cedro Ridge, Las Alturas Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km NE of San Vito near Alturas, surroundings of station and trail into forest; 82° 50' W, 8° 57' N, 1600 m; montane rain forest zone, pasture with group of trees bordering forest, on bark (lower trunk), semi-exposed; Jun 2002, *Sipman 47813d* (B).

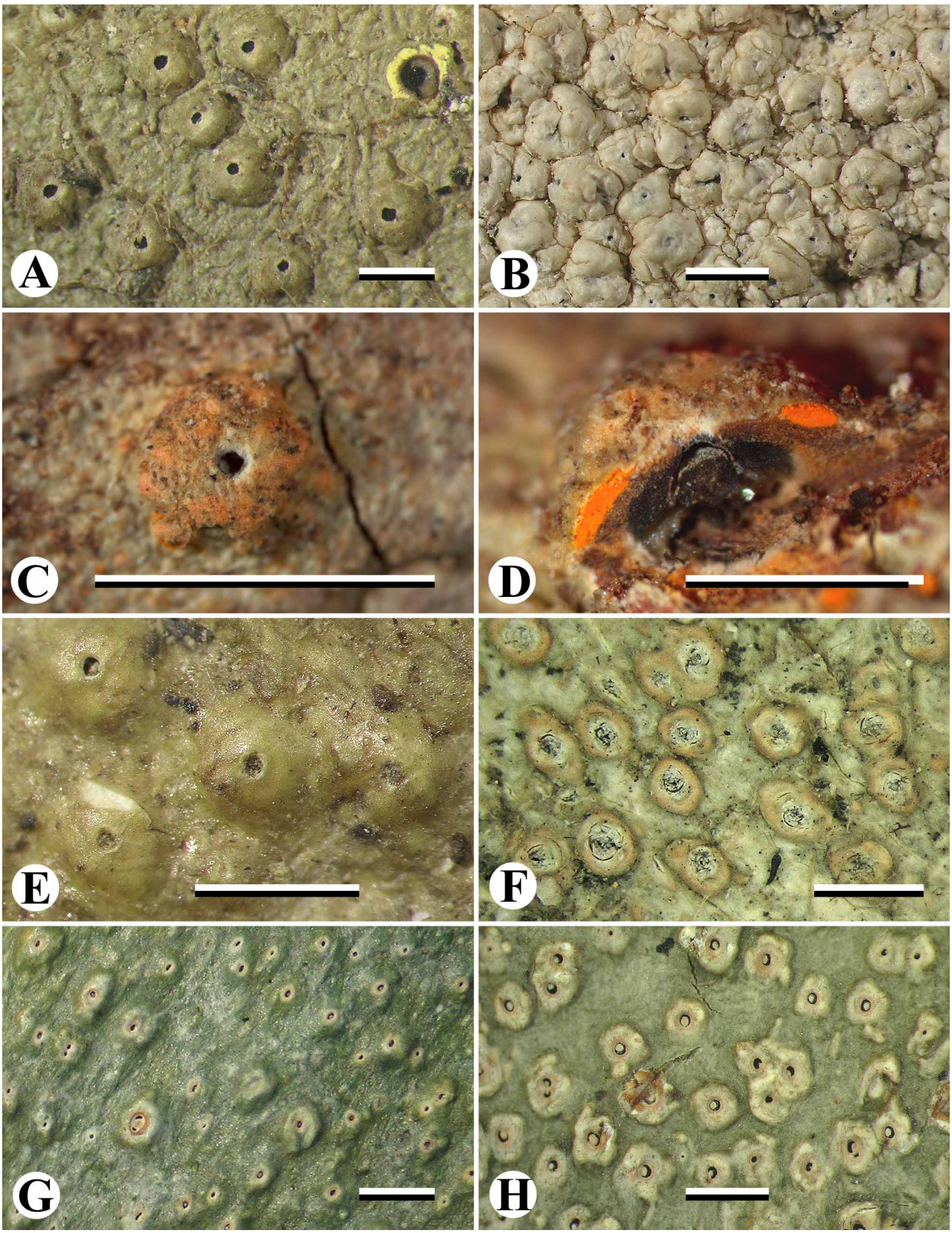

FIGURE 21. A. *Ocellularia cavata*. B. *Ocellularia chiriquiensis*. C–D. *Ocellularia cocosensis*. E. *Ocellularia conformis*. F. *Ocellularia crocea*. G–H. *Ocellularia cryptica*. Scale = 1 mm except D = 0.5 mm.

***Ocellularia chiriquiensis* (Hale) Hale** (Fig. 21B)

Ocellularia chiriquiensis (Hale) Hale, Mycotaxon 11: 136 (1980); *Leptotrema chiriquiense* Hale, Smithson. Contr. Bot. 38: 50 (1978). Holotype. Panama, *Hale 46035* (US!).

Thallus light grey-olive, verrucose, with dense, paraplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent to sessile, angular-rounded, 0.7–1 mm diam.; disc covered by narrow, 0.1 mm wide pore, invisible; margin entire, yellow-white, laterally covered by thalline layer. Columella absent. Excipulum prosoplectenchymatous, apically dark brown; periphysoids absent. Hymenium 250–350 µm high, clear; paraphyses unbranched. Ascospores 1–2/ascus, richly muriform, 160–250 × 35–50 µm, oblong, with slightly thickened septa and rectangular lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids.

Remarks:—*Ocellularia chiriquiensis* is one of several ecolumellate species with large, muriform ascospores and hypoprotocetraric acid. It is the only species with distinctly brown ascospores in that group. Most similar is *O. eumorpha* (Stirt.) Hale, which has an apically carbonized excipulum and pale brown ascospores. *Ocellularia inthanonensis* Homchantara & Coppins, with consistently colorless ascospores (Papong *et al.* 2010), is probably conspecific with *O. eumorpha*. *Ocellularia eumorphoides* Frisch differs from these taxa in the pale brown excipulum and partially developed columella.

Specimens examined:—COSTA RICA. Cartago: Interamerican Highway, 11 km S of Cartago; 9° 48' N, 83° 55' W, 1650 m; on bark in a lower montane rainforest; Dec 1978, *Kalb & Plöbst 38921* (hb. Kalb). Puntarenas: Fila Cruces Ridge, surroundings of Las Cruces Tropical Botanical Garden, 4 km SSE of San Vito; 8° 43' N, 82° 58' W, 1550 m; in a premontane rainforest at a waterfall; Jan 1979, *Kalb & Plöbst 38922* (hb. Kalb). San José: Cordillera de Talamanca, Interamerican Highway near El Empalme, S side of the highway to San Pablo; 9° 13' N, 83° 37' W, 2200 m; lower mountain rainforest; Dec 1978, *Kalb & Plöbst 32991* (hb. Kalb).

Ocellularia cocosensis* Lücking, *spec. nov. (Fig. 21C–D)
MycoBank #800082

Differing from *Ocellularia mordenii* in the columellate apothecia.

Holotype:—COSTA RICA. Puntarenas: Cocos Island National Park, Wafer Bay, 500 km SW of Costa Rica, trail above ranger station; 87° 04' W, 5° 31' N, 100 m; lowland rain forest zone, closed primary forest, on bark (branch), partially shaded; Apr 1992, *Lücking s.n.* (F).

Thallus light grey-olive, smooth to uneven, with loose cortex; medulla cinnabar-red; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 1–2 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, filled by brown-black, white-pruinose columella; margin entire, brown-black, white-pruinose, laterally covered by thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 250–350 µm high, clear; paraphyses unbranched. Ascospores 2–4/ascus, 21–39-septate, 150–250 × 15–25 µm, oblong, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC; medulla with cinnabar-red (K+ purple) anthraquinone.

Remarks:—This new species is characterized by the columellate, carbonized apothecia, large multiseptate ascospores, and the cinnabar-red medulla. It agrees in all aspects with *Ocellularia mordenii* (see below), but the latter lacks a columella. *Ocellularia fecunda* (Vain.) Hale differs from *O. cocosensis* in the pale yellow medulla. Another similar species is *Ocellularia gracilis* Müll. Arg., which has an orange medulla and shorter ascospores.

***Ocellularia conformis* (Feé) Hale** (Fig. 21E)

Ocellularia conformis (Fée) Hale, Mycotaxon 11: 136 (1980); *Thelotrema conforme* Fée, Essai Crypt. Exot., Suppl.: 89 (1837). Lectotype (Hale 1974: 32). "America meridionali", s.col. (G!).
Thelotrema consanguineum Müll. Arg., Flora 70: 398 (1887). Lectotype (Hale 1978: 42). Brazil, *Puiggari 477* (G!).

Thallus light grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.7–1 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, filled by brown-black, white-pruinose columella; margin entire, yellow-white, laterally covered by thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, upper half carbonized; periphysoids absent. Hymenium 100–150 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, muriform, 25–50 × 10–16 µm, ellipsoid, with thick septa and rounded lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This species belongs in a group of taxa with psoromic acid and erumpent apothecia with narrow pore. Among these, *Ocellularia conformis* is characterized by columellate, carbonized apothecia and muriform ascospores. The newly described *O. subcarassensis* (see below) lacks a columella, whereas the closely related *O. terebrata* has smaller, transversely septate ascospores.

Specimens examined:—COSTA RICA. Puntarenas: Surroundings of Las Cruces Tropical Botanical Garden, 4 km SSE of San Vito; 8° 43' N, 82° 58' W, 1500 m; in a premontane rainforest; Jan 1979, *Kalb & Plöbst 38919* (hb. Kalb).

***Ocellularia crocea* (Kremp.) Overeem & D. Overeem** (Fig. 21F)

Ocellularia crocea (Kremp.) Overeem & D. Overeem, Bull. Jard. Bot. Buitenzorg, Ser. 3, 4: 118 (1922); *Ascidium croceum* Kremp., Nuov. Giorn. Bot. Ital. 7: 25 (1875). Lectotype (Hale 1978: 17). Malaysia (Borneo), *Beccari 31c* (M!).

Thallus light grey-yellow-brown, smooth to uneven, with dense, prosoplectenchymatous cortex; medulla orange; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.4–0.7 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, invisible; margin entire to fissured, orange, laterally covered by thalline layer. Columella absent. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–5-septate, 18–25 × 5–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: cinchonarum unknowns; medulla with orange (K+ purple) anthraquinone.

Remarks:—This species belongs in *Ocellularia* s.str. and is close to the generic type, *O. cavata*. Contrary to the latter, in *O. crocea* the apothecial margin is typically fissured-lobulate and sometimes makes the impression of being finely layered. This provides a transition towards the genus *Gyrotrema*, which appears to be sister to *Ocellularia* s.str. (Rivas Plata *et al.* 2012b) but has large, chroodiscoid, pigmented apothecia with concentric rings of older excipula and hymenia. *Ocellularia crocea* was synonymized with *O. cavata* by Mangold *et al.* (2009) but differs in important features: the fissured apothecial margin, the lack of a columella, the distinctly smaller ascospores, and the deep (not pale) orange medullary pigment.

Specimens examined:—The species has been reported from Panama (Hale 1978).

Ocellularia cryptica* Lücking, *spec. nov. (Fig. 21G–H)
MycoBank #800083

Differing from *Ocellularia mauritiana* and *O. perforata* in the larger ascospores.

Holotype:—COSTA RICA. Puntarenas: La Amistad International Park, Altamira Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 20 km N of San Vito near Finca Colorado, interpretative trail (Sendero Gigantes) behind station; 83° 00' W, 9° 02' N, 1500–1600 m; montane rain forest zone, disturbed primary forest and secondary vegetation dominated by *Cecropia*, on bark (lower stem), partially shaded; Jun 2002, *Lücking 15215* (INB-0003976136; isotypes: F, USJ).

Thallus grey-olive-yellow, smooth to uneven, with dense, paraplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, angular-rounded, 0.5–1 mm diam.; disc partially covered by 0.2–0.5 mm wide pore, flesh-colored, partly filled by brown columella; margin entire, brown to yellow-white, laterally covered by thalline layer. Columella present, irregular, brown. Excipulum prosoplectenchymatous, brown; periphysoids absent. Hymenium 100–130 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 7–9-septate, 35–45 × 8–10 µm, oblong-ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: protocetraric and virensic acids.

Remarks:—This is a good example of a semi-cryptic species (hence the epithet), as without molecular data it would have been identified as *Ocellularia mauritiana* or *O. perforata* (see below); however, molecular data place it separate from these species (Rivas Plata *et al.* 2012b). The ascospores are larger than in *O. mauritiana* and *O. perforata*, but otherwise, the differences are spurious and many workers would consider the differences in ascospore size as intraspecific variation. There are otherwise a large number of species in *Ocellularia* with protocetraric acid, hyaline, transversely septate ascospores, and non-carbonized excipulum and columella. *Ocellularia auberianoides* (Nyl.) Müll. Arg. and *O. bonplandii* Spreng. have a minutely grainy thallus and smaller ascospores. *Ocellularia cameroonensis* Frisch has smaller ascospores. *Ocellularia vezdana* (see below) differs in its very small ascospores and pale excipulum and columella, the latter being usually present in part of the apothecia only.

Additional specimens examined (paratypes):—COSTA RICA. Puntarenas: La Amistad International Park, Altamira Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 20 km N of San Vito near Finca Colorado, interpretative trail (Sendero Gigantes) behind station; 83° 00' W, 9° 02' N, 1500–1600 m; montane rain forest zone, disturbed primary forest and secondary vegetation dominated by *Cecropia*, on bark (lower trunk), semi-exposed; Jun 2002, *Sipman 48034c* (B, INB); ibid., trail to Casa Coca; 83° 00' W, 9° 02' N, 1600–1800 m; montane rain forest zone, secondary forest and open secondary vegetation dominated by *Cecropia*, on bark (lower trunk), partially shaded; Jul 2002, *Sipman 48045a* (B, INB). Wilson Botanical Garden, Las Cruces Biological Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 190 km SE of San José, trail beyond botanical garden; 82° 58' W, 8° 47' N, 1200 m; montane rain forest zone, primary forest, on bark (lower trunk), fully shaded; Sep 2007, *Lücking 21068* (F).

***Ocellularia decolorata* Hale** (Fig. 22A)

Ocellularia decolorata Hale, Smithson. Contr. Bot. 38: 19 (1978). Holotype: Panama, *Hale 43462* (US!).

Thallus grey-olive-yellow, smooth to uneven, with dense cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent to prominent, angular-rounded, 0.4–0.6 mm diam.; disc covered by narrow, 0.1 mm wide pore and inner layers of excipulum, invisible; proper margin fissured to lobulate, yellow-white, layered, laterally covered by thalline layer. Columella absent. Excipulum prosoplectenchymatous, apically dark brown; periphysoids absent. Hymenium 100–120 µm high, clear;

paraphyses unbranched. Ascospores 8/ascus, 3–5-septate, 18–24 × 5–7 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: cinchonarum unknown.

Remarks:—Due to the layered, fissured excipulum, this species looks superficially similar to certain species of *Chapsa* (*C. laceratula*) and *Schizotrema*, but the ascospore type and chemistry would place it within *Ocellularia*. Hale (1978) compared it with *O. crocea*, which also has a layered excipulum and is akin towards the genus *Gyrotrema* (Rivas Plata *et al.* 2012b). It is possible that *O. decolorata* represents another lineage within *Ocellularia* s.lat. that evolved apothecia with concentrically layered excipulum. On the other hand, Mangold *et al.* (2009) reported cinchonarum unknown as the major substance for an undescribed species of *Schizotrema* close to *S. guadeloupense*.

Specimens examined:—Not yet known from Costa Rica, but reported from Panama (Hale 1978).

***Ocellularia dolichotata* (Nyl.) Zahlbr.** (Fig. 22B)

Ocellularia dolichotata (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 589 (1923); *Thelotrema dolichotatum* Nyl., Sertum Lich. Trop. Labuan Sing.: 19 (1891). Lectotype (Hale 1981: 303). Singapore, *Almquist s.n.* (H-NYL 22748!).

Thelotrema bataanum Vain., Ann. Acad. Sci. Fenn., Ser. A, 15(6): 188 (1921); Ocellularia bataana (Vain.) Zahlbr., Cat. Lich. Univ. 2: 583 (1923). Holotype. Philippines, *Robinson 6197* (TUR-VAIN 26874!).

Thelotrema siamense Vain., Hedwigia 46: 175 (1907); *Ocellularia siamensis* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 600 (1923). Lectotype (Hale 1981: 303). Thailand, *Schmidt s.n.* (TUR-VAIN 26866!).

Thallus light grey-green-yellow, verrucose, with dense, paraplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 1–1.5 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, filled by brown-black, white-pruinose columella; margin entire, yellow-white, laterally covered by thick thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 300–400 µm high, clear; paraphyses unbranched but laterally anastomosing. Ascospores single, 17–27-septate, 180–250 × 20–30 µm, fusiform, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Ocellularia dolichotata* is a unique species easily recognized by the columellate, carbonized apothecia, large multiseptate ascospores, and lack of lichen substances. Most similar is *Ocellularia allospora* (Nyl.) Zahlbr. which has brown, bicaudate ascospores. The species was thus far only known from the Palaeotropics. It is apparently a lowland rain forest species.

Specimens examined:—COSTA RICA. Limón: Hitoy Cerere Biological Reserve, Hitoy Cerere Biological Station (La Amistad Caribe Conservation Area), Talamanca Ridge, 125 km ESE of San José, 40 km S of Limón, near Pandora, trail adjacent to access road before station; 83° 02' W, 9° 40' N, 150–200 m; lowland to lower montane rain forest zone, disturbed primary and oldgrowth secondary forest, on bark (upper trunk, fallen), exposed; Mar 2004, *Lücking 17054c* (F, INB). Puntarenas: Carara Biological Reserve, 15 km SSW of Orotina; 84° 37' W, 9° 47' N, 50 m; disturbed primary, c. 40 m tall forest, along trail near warden's house, on fallen tree; Nov 1988, *Sipman & Döbbeler 42231* (B, CR), *42242* (B, CR). Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, first part of trail from Sirena to Los Patos Station; 83° 35' W, 8° 30' N, sea level; lowland rain forest zone, primary forest remnants and closed secondary forest, on bark (lower trunk), semi-exposed; Apr 2003, *Buck 44104* (F, INB, NY); ibid., round trail NW of station (Sendero Sirena and Sendero Guanacaste); 83° 35' W, 8° 29' N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (lower stem), partially shaded; Apr 2003, *Sipman 51158* (B, CR), *51167b* (B, INB), *51175c* (B, INB).

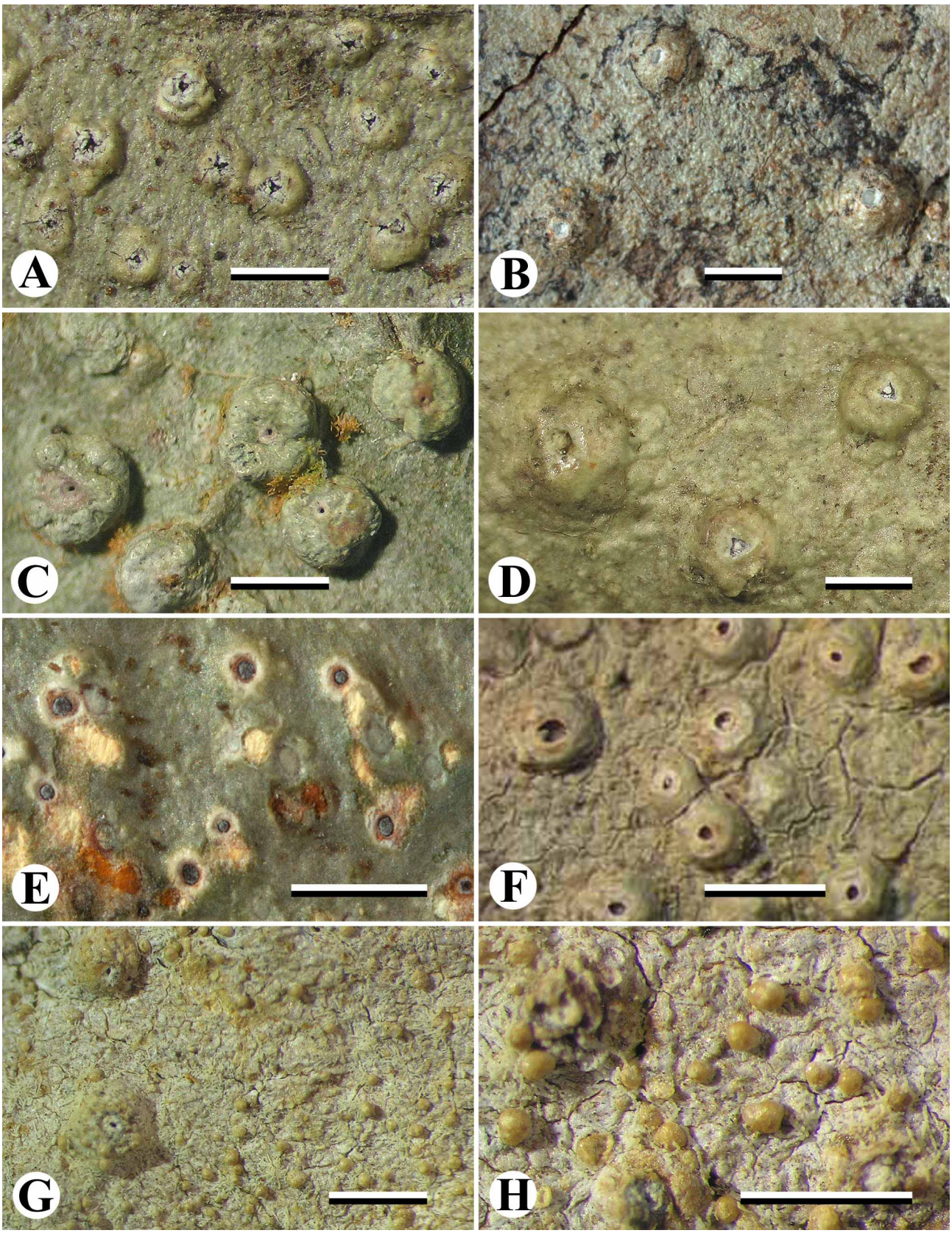

FIGURE 22. A. *Ocellularia decolorata*. B. *Ocellularia dolichotata*. C. *Ocellularia domingensis*. D. *Ocellularia fecunda*. E. *Ocellularia flavoperforata*. F. *Ocellularia gerardii*. G–H. *Ocellularia globifera*. Scale = 1 mm.

***Ocellularia domingensis* (Feé ex Nyl.) Müll. Arg.** (Fig. 22C)

Ocellularia domingensis (Fée in Nyl.) Müll. Arg., Flora 70. 398, 1887; *Ascidium domingense* Fée in Nyl., Mém. Soc. Sci. Nat. Cherbourg 5: 118 (1857); Nylander, Acta Soc. Sci. Fenn. 7: 455 (1863); *Thelotrema domingense* (Fée) Tuck., Syn. N. Amer. Lich. 1: 225 (1882). Neotype (Hale 1978: 20). Colombia, *Lindig 2683* (FH!; isoneotypes: BM!, UPS!).

Thallus light grey-yellow-brown, verrucose, with dense, paraplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia sessile, rounded, 0.8–1 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, rarely filled by brown-black, white-pruinose columella; margin entire, yellow-white, laterally covered by thick thalline layer. Columella absent or rarely present, simple, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 250–350 µm high, clear; paraphyses unbranched. Ascospores 1–2/ascus, 19–39-septate, 80–250 × 20–40 µm, fusiform, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids.

Remarks:—*Ocellularia domingensis* belongs in a difficult complex of species with carbonized apothecia, large multiseptate ascospores and the hypoprotocetraric acid chemosyndrome. Most similar is *O. neopertusariiformis* Hale, which only appears to differ in the 2–8-spored asci. *Ocellularia henatomma* (Ach.) Müll. Arg. regularly produces a columella and has prominent rather than sessile apothecia and slightly smaller ascospores in numbers of (1–)2–4/ascus. *Ocellularia triglyphica* (Kremp.) Overeem & Overeem and *O. granulifera* (Kremp.) Müll. Arg. are also similar but have 2-hydroxy-hypoprotocetraric acid as major secondary compound, with *O. triglyphica* having 8 ascospores per ascus and *O. granulifera* 2–4. Both agree with *O. henatomma* in the prominent, not sessile, apothecia and the regular occurrence of a columella. This complex requires further study. *Ocellularia domingensis* also differs from the other three taxa in being typically found at higher elevations.

Specimens examined:—COSTA RICA. Cartago: Chirripó National Park, trail from San Gerardo to Base Crestones, Filo Cementerio de la Máquina; 83° 29' W, 9° 29' N, 2400 m; mossy mountain forest, disturbed primary forest, on trunk along trail; Mar 2000, *Sipman & Umaña 46504* (B, INB); ibid., trail from Base Crestones to San Gerardo; 83° 29' W, 9° 29' N, 2500 m; disturbed primary mossy mountain forest, on trunk along trail; Mar 2000, *Sipman & Umaña 46574* (B, INBio). Puntarenas: Wilson Botanical Garden, Las Cruces Biological Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 190 km SE of San José, trail beyond botanical garden; 82° 58' W, 8° 47' N, 1200 m; montane rain forest zone, primary forest, on bark (lower trunk), fully shaded; Sep 2007, *Lücking 21078* (F). San José: San Gerardo de Dota, Cordillera de Talamanca, ca. 5 km W of Cerro de la Muerte, along Quebrada Ojo de Agua; 83° 48' W, 9° 35' N, 2600 m; epiphyte; Mar 1985, *Sipman & Chaverri 20775* (B, CR), *20784* (B, CR).

***Ocellularia fecunda* (Vain.) Hale** (Fig. 22D)

Ocellularia fecunda (Vain.) Hale, Smithson. Contr. Bot. 16: 20 (1974); *Thelotrema domingense* var. *fecundum* Vain., J. Bot. 34: 208 (1896). Lectotype (Hale 1974: 20). Lesser Antilles (St. Vincent), *Elliott 243* (BM!; isolectotype: TUR-VAIN 26856!).

Thallus light grey-green, verrucose, with dense, paraplectenchymatous cortex; medulla pale yellow; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 1–2 mm diam.; disc covered by narrow, 0.2–0.4 mm wide pore, filled by brown-black, white-pruinose columella; margin verrucose, pale brown, laterally covered by thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 200–300 µm high, clear; paraphyses unbranched. Ascospores 1–4/ascus, 15-29-septate, 80–190 × 12–20 µm, oblong, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids, medulla with pale yellow (K+ red) pigment.

Remarks:—This species is identical to *Ocellularia henatomma* except for the presence of a pale yellow medullary pigment.

Specimens examined:—*Ocellularia fecunda* is know yet known from Costa Rica but has been reported from Panama (Hale 1978).

Ocellularia flavoperforata* Lücking, *spec. nov. (Fig. 22E)
MycoBank #800084

Differing from *Ocellularia perforata* in the pale yellow medullary pigment.

Holotype:—COSTA RICA. Puntarenas: Wilson Botanical Garden, Las Cruces Biological Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 190 km SE of San José, trail beyond botanical garden; 82° 58' W, 8° 47' N, 1200 m; montane rain forest zone, primary forest, on bark (lower trunk), fully shaded; Sep 2007, *Lücking 21073c* (F).

Thallus light grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex; medulla pale yellow; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.3–0.5 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, filled by brown-black columella; margin entire, red-brown, laterally covered by thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, red-brown; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–7-septate, 20–25 × 6–9 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids (exposed medulla P– but masked by pigment reaction; section K– but masked by pigment reaction; TLC!), medulla with pale yellow (K+ red) pigment.

Remarks:—This new species is identical to *Ocellularia perforata* in all aspects but differs in the pale yellow medulla. This is the first pigmented species known in the *O. papillata* group.

Ocellularia gerardii* Sipman, *spec. nov. (Fig. 22F)
MycoBank #800085

Differing from *Ocellularia psorbarroensis* in the absence of columella structured and the presence of additional stictic acid.

Holotype:—COSTA RICA. San José: San Gerardo de Dota, Cordillera de Talamanca, ca. 5 km W of Cerro de la Muerte, along Quebrada Ojo de Agua; 9° 35' N, 83° 48' W, 2600 m; Mar 1985, *Sipman & Chaverri 20796* (B; isotype: CR).

Thallus grey-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.3–0.6 mm diam.; disc partially covered by 0.1–0.3 mm wide pore, flesh-colored to pale brown, white-pruinose; margin entire, pale brown, laterally covered by thalline layer. Columella absent. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 100–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5-septate, 15–20 × 4–6 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic and stictic acids.

Remarks:—This is another uncarbonized species of *Ocellularia*, named after the type locality of San Gerardo de Dota. It differs from other species in the *Ocellularia* clade with small, transversely septate ascospores, uncarbonized ascocarps and psoromic acid by the prominent apothecia and the additional presence of stictic acid. The most similar species either have immersed, myriotremoid apothecia, such as *Myriotrema clandestinum*, or some form of columella present, such as *O. psorbarroensis* (see below). The

chemistry of psoromic plus stictic acid is unusual and there are few other species with such a chemistry, including *Myriotrema mammillare* (Hale) Hale and *M. uniseptatum* Hale; both differ from *Ocellularia gerardii* in several morphological and anatomical features.

Ocellularia globifera* Kalb & Lücking, *spec. nov (Fig. 22G–H)**.**
MycoBank #800086

Differing from *Ocellularia interposita* in the transversely septate ascospores and globose isidia.

Holotype:—COSTA RICA. Puntarenas: Surroundings of Las Cruces Tropical Botanical Garden, 4 km SSE of San Vito; 8°43' N, 82°58' W, 1500 m; premontane rain forest; Jan 1979, *Kalb & Plöbst 38945* (hb. Kalb).

Thallus light grey-olive-yellow, uneven to finely plicate, with dense, paraplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals, isidiate; isidia scattered, subglobose, up to 0.15 mm wide and high, yellow-brown. Apothecia prominent, rounded, 0.7–1.1 mm diam.; disc covered by narrow, 0.05–0.1 mm wide pore; margin entire, pale brown, laterally covered by thick thalline layer. Columella absent. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 250–350 µm high, clear; paraphyses unbranched but laterally anastomosing. Ascospores 1/ascus, 19–29-septate, 130–250 × 30–50 µm, fusiform, with thick septa but almost rectangular lumina, and thick wall, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic acid.

Remarks:—This new species is one of few in the genus producing isidia which, in contrast to other species, are short and subglobose. Two other species have psoromic acid and isidia: *O. isidioalbula* Mangold has small ascospores and an uncarbonized excipulum, in addition to an irregular pseudocolumella, whereas an undescribed species related to *O. profunda* (Stirt.) Mangold, Elix & Lumbsch differs in its muriform ascospores. The only species in the genus with psoromic acid and large, transversely septate ascospores, *O. canariana* Patw., Sethy & Nagarkar and *O. ripleyi* (see below), lack isidia and have a columella.

Ocellularia inspersata* Kalb & Lücking, *spec. nov. (Fig. 23A)
MycoBank #800087

Differing from *Ocellularia psorbarroensis* in the inspersed hymenium and submuriform ascospores.

Holotype:—COSTA RICA. Puntarenas: Cordillera de Tilarán, Monteverde, surroundings of the Hotel de la Montaña; 10°18' N, 84°49' W, 1500 m; lower montane rain forest; Jan 1979, *Kalb & Plöbst 38941* (hb. Kalb).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded to angular, 0.5–0.9 mm diam.; disc covered by 0.2–0.4 mm wide pore; margin entire or rarely fissured, white-yellow, laterally covered by thalline margin. Pseudocolumella sometimes present, irregular, white. Excipulum prosoplectenchymatous, brown to dark brown; periphysoids absent. Hymenium 120–150 µm high, inspersed; paraphyses unbranched. Ascospores 8/ascus, submuriform with 5–7 transverse and 0–2 longitudinal septa per segment, 20–32 × 10–12 µm, oval, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This is another new species with the unusual combination of an inspersed hymenium, submuriform ascospores, and psoromic acid. It is the first species known in the genus that combines an inspersed hymenium with either submuriform ascospores or psoromic acid. *Ocellularia inspersata* seems to be most closely related to the group formed by *O. barroensis*, *O. psorbarroensis*, and *O. pluriporoides*, which all differ in having a clear hymenium and transversely septate ascospores. Also similar is the newly described *O. inspersula*, which agrees in the inspersed hymenium but has transversely septate ascospores and produces protocetraric acid. The newly described *O. subcarassensis* (see below) agrees with *O. inspersata* in most aspects but has a clear hymenium and slightly larger ascospores.

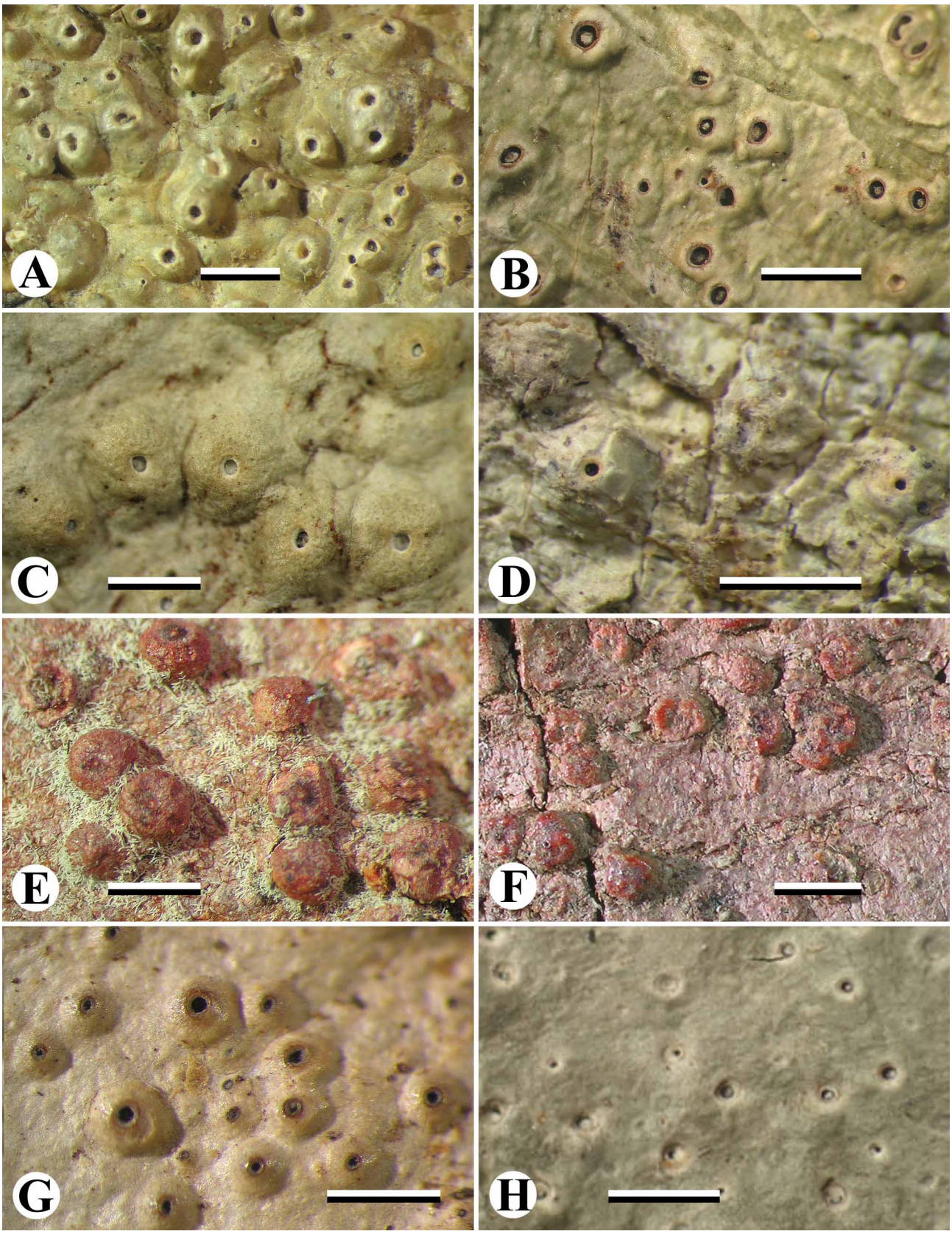

FIGURE 23. A. *Ocellularia inspersata*. B. *Ocellularia inspersula*. C. *Ocellularia interposita*. D. *Ocellularia inturgescens*. E–F. *Ocellularia isohypocrellina*. G. *Ocellularia laevigatula*. H. *Ocellularia laeviusculoides*. Scale = 1 mm.

Ocellularia inspersula* Lücking & Aptroot, *spec. nov. (Fig. 23B)
MycoBank #800088

Differing from *Ocellularia mauritiana* in the inspersed hymenium and smaller ascospores.

Holotype:—COSTA RICA. Puntarenas: Las Tablas Protection Zone, Cedro Ridge, Las Alturas Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km NE of San Vito near Alturas, surroundings of station and trail into forest; 82° 50' W, 8° 57' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower stem), fully shaded; Jun 2002, *Lücking 15077i* (INB-0003953257; isotypes: F, USJ).

Thallus light grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.6–0.8 mm diam.; disc partially covered by 0.2–0.4 mm wide pore, flesh-colored, partially filled by white pseudocolumella; margin entire, yellow-white, laterally covered by thalline layer. Pseudocolumella present, irregular, colorless. Excipulum prosoplectenchymatous, brown; periphysoids absent. Hymenium 80–100 µm high, inspersed; paraphyses unbranched. Ascospores 8/ascus, 3–5-septate, 10–16 × 5–6 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet (amyloid). Secondary chemistry: protocetraric and virensic acids.

Remarks:—This is one of few species with inspersed hymenium in the genus *Ocellularia*. All other known species differ in apothecial anatomy, ascospore type, and/or secondary chemistry. The species is most similar to the non-inspersed *O. mauritiana* and *O. perforata* (see below). The first has also larger, more prominent apothecia and larger ascospores, whereas the second has dark brown excipulum and columella and much larger ascospores.

Additional specimens examined:—COSTA RICA. Puntarenas: Las Tablas Protection Zone, Cedro Ridge, Las Alturas Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km NE of San Vito near Alturas, surroundings of station and trail into forest; 82° 50' W, 8° 57' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower stem), fully shaded; Jun 2002, *Lücking 15077e* (INB-0003953249).

***Ocellularia interposita* (Nyl.) Hale** (Fig. 23C)

Ocellularia interposita (Nyl.) Hale, Mycotaxon 11: 137 (1980); *Ascidium interpositum* Nyl., Ann. Sci. Nat. Bot., Ser. 4, 19: 336 (1863). Lectotype (Hale 1974: 35). Cuba, *Wright 28* (H-NYL!; Wright, Lich. Cubae 164; isolectotypes: BM!, FH!, M!, UPS!).
Thelotrema turgidulum Vain., Bol. Soc. Brot., Ser. 2, 6: 150 (1929–1930). Holotype. Mozambique, *Lima 160* (TUR-VAIN 34811!).

Thallus grey-olive-yellow, verrucose-bullate, with dense, paraplectenchymatous cortex; photobiont layer and medulla with columnar clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.7–1.6 mm diam.; disc covered by narrow, 0.15–0.2 mm wide pore, filled by brown-black, white-pruinose columella; margin entire, pale brown, laterally covered by thick thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 200–300 µm high, clear; paraphyses unbranched but laterally anastomosing. Ascospores 1–2/ascus, richly muriform, 100–200 × 30–40 µm, ellipsoid, with slightly thickened septa and rectangular lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This species is characterized by a verrucose thallus, robust, columellate and carbonized apothecia, large muriform ascospores, and psoromic acid. There are a number of similar species: *Ocellularia profunda* (Stirt.) Mangold, Elix & Lumbsch and *O. megalospora* Müll. Arg. have ascospores almost twice as large. *Ocellularia bicuspidata* (Müll. Arg.) Mangold, Elix & Lumbsch, *O. maxima* (see below) and *O.*

postposita (see below) differ mainly in their thallus structure, the first having a loose cortex (in addition to bicaudate ascospores) and the latter two having a smooth thallus with prosoplectenchymatous cortex. *Ocellularia piperis* (Vain.) Aptroot is morphologically very similar to these species but has hypoprotocetraric acid as secondary substance. *Ocellularia interposita* appears to be a lowland species.

Specimens examined:—COSTA RICA. Puntarenas: Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), partially shaded; Feb 1997, *Lücking 97-126* (F), *97-154a* (CR, F).

***Ocellularia inturgescens* (Müll. Arg.) Mangold** (Fig. 23D)

Ocellularia inturgescens (Müll.Arg.) Mangold in Mangold *et al.*, Fl. Australia 57: 656 (2009); *Thelotrema inturgescens* Müll. Arg., Hedwigia 32: 131 (1893). Holotype. Australia, *Bailey 1552* (G!; isotypes: BRI!, US!).
Thelotrema exile Hale, Mycotaxon 7: 381 (1978); *Myriotrema exile* (Hale) Hale, Mycotaxon 11: 133 (1980). Holotype. Malaysia, *Hale 28249* (US!).

Thallus grey-olive-yellow, uneven to verrucose, with dense, paraplectenchymatous cortex; photobiont layer and medulla with columnar clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.5–1 mm diam.; disc covered by narrow, 0.15–0.2 mm wide pore; margin entire, yellow-white, laterally covered by thick thalline layer. Columella absent. Excipulum prosoplectenchymatous, yellow- to orange-brown; periphysoids absent. Hymenium 250–500 µm high, clear; paraphyses unbranched but laterally anastomosing. Ascospores 1(–2)/ascus, richly muriform, 150–400 × 30–50 µm, fusiform, with slightly thickened septa and rectangular lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—The present material has been tentatively identified with this species as it differs in the thinner thallus with irregular clusters of crystals and more prominent apothecia. However, in the remaining characters, especially the non-columellate, uncarbonized apothecia, large muriform ascospores, and psoromic acid, there is no other comparable species in the family, and the differences towards other studied material of *Ocellularia inturgescens* (types and material from Australia), the differences are too small to risk establishing a new species based on a single collection. Superficially similar species include *Ocellularia interposita* (see above) and *O. postposita* (Nyl.) Frisch, but these differ by the columellate, carbonized apothecia.

Specimens examined:—COSTA RICA. San José: San Gerardo de Dota, Finca Chacón, near entrance of Sendero La Quebrada; 83° 48.3' W, 9° 32.9' N, 2800 m; mixed, light, primary *Quercus* forest on steep slope, on sapling; Nov 1999, *Sipman 44329* (B 60 0163795), *44330* (B 60 0163794).

Ocellularia isohypocrellina* Lücking & Kalb, *spec. nov. (Fig. 23E–F)
MycoBank #800089

Differing from *Ocellularia rhodostroma* in the ascospores becoming brown and the pockets of dark red pigment in the medulla.

Holotype:—COSTA RICA. Puntarenas: Surroundings of Las Cruces Tropical Botanical Garden, 4 km SSE of San Vito; 1300 m; premontane rainforest; Dec 1978, *Kalb & Plöbst 31808* (hb. Kalb). Paratype. Puntarenas: South of Las Cruces Botanical Garden, 5 km S of San Vito, Fila Cruces Ridge; 82° 57' W, 8° 43' N, 1200–1600 m; premontane forest zone; along road and at edge of cut forest; Dec 1978, *Wetmore 36941* (MIN).

Thallus light grey-olive, mottled dark red, uneven, with dense cortex; medulla thin, with pockets of dark red crystals, in the apothecial margins also pink. Apothecia prominent, rounded to irregular, 0.8–1.2 mm diam.; disc covered by narrow, 0.05–0.1 mm wide pore; margin entire, brown-black, laterally covered by

thalline layer, uneven to verrucose. Columella absent. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 200–250 µm high, clear; paraphyses unbranched. Ascospores 1/ascus, 21–29-septate, in part becoming submuriform with 0–1 longitudinal septa per segment, 120–170 × 18–25 µm, narrowly fusiform, with thickened septa and angular to lens-shaped lumina, brown when mature, I+ violet-blue (amyloid) when young. Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids, medulla in apothecial margins with pink (K+ aeruginous) pigment, in thallus mottled with dark red (K+ yellow-green) isohypocrellin.

Remarks:—This appears to be the first genuine *Ocellularia* species with the dark red pigment isohypocrellin, in addition to the pink medulla in the apothecial margins. Other species with pink medulla differ in the absence of isohypocrellin, consistently hyaline ascospores, and other details: the closely related *O. rhodostroma* (see below) has smooth apothecial margins, *O. americana* Hale has a columella and produces gyrophoric acid, and *O. roseotecta* Homchantara & Coppins has a broad-stump-shaped columella and produces an unknown substance. There are only two other species in the genus with large, transversely septate, brown ascospores and one with large, muriform, brown ascospores, viz. *O. eumorpha* (Stirt.) Hale, *O. jamesii* (Patw.) & C. R. Kulk.) D. D. Awasthi, and *O. allospora* (Nyl.) Zahlbr. All three lack pigments and *O. allospora* has a columella and columnar clusters of calcium oxalate crystals in the thallus, whereas *O. jamesii* has smaller, erumpent apothecia. *Ocellularia eumorpha* has distinctly muriform ascospores. The partly submuriform ascospores in *O. isohypocrellina* are strange as they have mostly been observed in immature, hyaline ascospores, whereas the mature, brown ascospores are typically transversely septate only.

Ocellularia laevigatula* Kalb & Lücking, *spec. nov. (Fig. 23G)
MycoBank #800090

Differing from *Ocellularia bahiana* in the smooth thallus and fusiform ascospores.

Holotype:—COSTA RICA. Puntarenas: Surroundings of Las Cruces Tropical Botanical Garden, 4 km SSE of San Vito; 8°43’ N, 82°58’ W, 1300 m; premontane rainforest; Dec 1978, *Kalb & Plöbst 38948* (hb. Kalb).

Thallus light grey-olive-yellow, smooth, with dense, paraplectenchymatous cortex; photobiont layer and medulla with scattered clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.4–0.7 mm diam.; disc covered by 0.1–0.3 mm wide pore, brown-black, thinly white-pruinose; margin entire, brown, laterally covered by thick thalline layer. Columella absent. Excipulum prosoplectenchymatous, upper half brown; periphysoids absent. Hymenium 100–120 µm high, clear; paraphyses unbranched, thick. Ascospores 8/ascus, muriform, 30–40 × 12–15 µm, fusiform, with thickened septa and angular-rounded lumina, brown, young I+ violet (amyloid). Secondary chemistry: protocetraric and virensic acids.

Remarks:—Although this material is rather non-descript, we have not found a published epithet for this taxon. The brown ascospores, together with the protocetraric acid chemistry, suggest a relationship to the *Ocellularia bahiana* group. There are four species in this group with the same chemistry and similar ascospores: *O. bahiana* (see above), *O. obturascens* (see below), and *O. petrinensis* J. C. David, all have a minutely grainy thallus caused by columnar clusters of crystals in the photobiont layer and medulla; the first two species also have larger apothecia with wider pores. *Myriotrema permaculatum* Nagarkar & Hale has a similar thallus anatomy as *O. laevigatula* but the thallus and apothecia are conspicuously scaly-verrucose.

Ocellularia laeviusculoides* Sipman & Lücking, *spec. nov. (Fig. 23H)
MycoBank #800091

Differing from *Ocellularia papillata* in the pale brown excipulum.

Holotype:—COSTA RICA. Puntarenas: Las Tablas Protection Zone, Cedro Ridge, Las Alturas Station (La

Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km NE of San Vito near Alturas, surroundings of station and trail into forest; 82° 50' W, 8° 57' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower trunk), semi-exposed; Jun 2002, *Sipman 47820f* (INB-0003908792; isotype: B).

Thallus light green-grey, smooth, with dense, prosoplectenchymatous cortex without internal splitting; photobiont layer and medulla with scattered clusters of calcium oxalate crystals. Apothecia immersed to erumpent, rounded, 0.3–0.6 mm diam.; disc covered by 0.2–0.4 mm wide pore, partially filled by brown-black, white-pruinose columella; margin entire, white to pale brown, laterally covered by thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous (pale) brown; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 7–9-septate, 20–30 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ dark violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Ocellularia laeviusculoides* is here segregated from *O. papillata* s.str., with which it shares the absence of lichen substances, presence of a carbonized columella and small, colorless, amyloid ascospores. It differs by the uncarbonized excipulum, which shows in abraded margins as a pale brown rather than dark brown ring, the ascocarps remaining mostly immersed, and the smoother thallus. The species is reminescent of *Myriotrema laeviusculum* (see above), but that taxon has protocetraric acid, an uncarbonized pseudocolumella, brown, muriform ascospores, and columnar crystals in the thallus.

Additional specimens examined (paratypes):—Costa Rica. Puntarenas: La Amistad International Park, Altamira Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 20 km N of San Vito near Finca Colorado, interpretative trail (Sendero Gigantes) behind station; 83° 00' W, 9° 02' N, 1500–1600 m; montane rain forest zone, disturbed primary forest and secondary vegetation dominated by *Cecropia*, on bark (lower trunk), partially shaded; Jun 2002, *Sipman 48016* (B, INB). Cordillera de Tilaran, Monteverde, near the cheese factory; 84° 49' W, 10° 18' N, 1450 m; premontane rain forest zone, forest relicts among pasturefields, on trunks; Jan 1979, *Sipman 12103* (U), *12124* (U).

***Ocellularia landronii* Hale** (Fig. 24A)

Ocellularia landronii Hale, Smithson. Contr. Bot. 38: 23 (1978). Holotype. Puerto Rico, *Landrón 358A* (US!).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent to prominent, angular-rounded, 0.8–1 mm diam.; disc partially covered by 0.3–0.5 mm wide pore, partly filled by brown-black, white-pruinose columella; margin fissured, brown-black, white-pruinose, marginally covered by thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–5-septate, 14–20 × 5–6 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Ocellularia landronii* resembles species of the *Stegobolus crassus* group but differs by the persistently simple columella and the absence of lichen substances. Also similar is *O. barroensis*, which has uncarbonized apothecia.

Specimens examined:—The species has not yet been found in Costa Rica but was reported from Panama by Hale (1978).

***Ocellularia mauritiana* Hale** (Fig. 24B)

Ocellularia mauritiana Hale, Mycotaxon 3: 175 (1975). Holotype. Mauritius, *Ayres s.n.* (BM!).
Ocellularia protocetrarica Hale, Smithson. Contr. Bot. 38: 28, 1978; *Myriotrema protocetraricum* (Hale) Hale,

Mycotaxon 11: 134 (1980). Holotype. Panama, *Hale 44786* (US!).

Thallus light grey-olive-yellow, smooth to uneven, with dense, paraplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, angular-rounded, 0.5–2 mm diam.; disc partially covered by 0.3–1 mm wide pore, flesh-colored, partly filled by brown columella; margin entire, brown to yellow-white, laterally covered by thalline layer. Columella present, irregular, brown. Excipulum prosoplectenchymatous, brown; periphysoids absent. Hymenium 90–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–7-septate, 19–25 × 7–9 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: protocetraric and virensic acids.

Remarks:—This taxon somewhat resembles *Ocellularia perforata* (see below) but differs in the larger, prominent apothecia with irregular columella in combination with smaller ascospores. *Ocellularia barroensis* and *O. psorbarroensis* are similar in external appearance but differ chemically (no substances or psoromic acid). In spite of their irregular columella, these species are not related to *Stegobolus* (Frisch & Kalb 2006; Rivas Plata *et al.* 2012b). *Ocellularia mauritiana* is one of the most widely distributed species in Costa Rica; it has mostly been found in wet rain forest at mid elevations. A somewhat aberrant specimen with larger apothecia and verrucose thallus is included here but might represent a separate taxon [Puntarenas: Wilson Botanical Garden, Las Cruces Biological Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 190 km SE of San José, trail beyond botanical garden; 82° 58' W, 8° 47' N, 1200 m; montane rain forest zone, primary forest, on bark (lower trunk), fully shaded; Sep 2007, *Lücking 21073a* (F)].

Specimens examined:—COSTA RICA. Alajuela: San Ramón Forest Reserve, near house at Río Lorencito, c. 5 km NE of Cerro Jabonal; 84° 37' W, 10° 13' N, 1000 m; humid, mossy forest with many ferns on mountain ridge, on thin trunk in undergrowth; Nov 1988, *Sipman et al. 41957* (B, CR). Guanacaste: Guanacaste Conservation area, Pitilla Biological Station, on humid E-slope of Volcan Orosi; 85° 26' W, 11° 00' N, 500 m, epiphyte in relic of primary forest near the station; Jun 1995, *Sipman 37284* (B, CR). Heredia: La Selva Protection Zone, La Selva Biological Station (Cordillera Volcánica Central Conservation Area), Volcánica Central Ridge, 55 km N of San Jose, trail behind laboratory (Sendero Oriental); 84° 03' W, 10° 26' N, 50 m; lowland rain forest zone, closed primary forest, on bark (branch, fallen) of Coussapoua, exposed; Jun 2002, *Lücking 15012f* (INB). Limón: Braulio Carrillo National Park, Quebrada Gonzales Section (Cordillera Volcánica Central Conservation Area), Volcánica Central Ridge, 30 km NNW of San José, trail below station (Sendero Natural Las Palmas); 83° 56' W, 10° 10' N, 400 m; lower montane rain forest zone, primary forest, on bark (lower trunk), partially shaded; March 2003, *Buck 44033* (INB, NY). San José: San Gerardo de Dota, Finca Chacón, near entrance of Sendero La Quebrada; 83° 48' W, 9° 33' N, 2800 m; mixed, light, primary *Quercus* forest on steep slope, on sapling; Nov 1999, *Sipman 44337* (B 60 0107621). Puntarenas: Near Las Cruzes Garden, c. 4 km SSE of San Vito; 82° 57' W, 8° 43' N, 1300 m; premontane rain forest zone, shady montane rain forest on slope near waterfall of Rio Jaba, on trunk; Jan 1979, *Sipman 11993* (U), *11996* (U). La Amistad International Park (Amistad Pacifico Conservation Area), Altamira station, 20 km N of San Vito near Finca Colorado, interpretative trail behind station (Sendero Gigantes); 83° 01' W, 9° 02' N, 1500–1600 m; montane rain forest zone, secondary vegetation dominated by *Cecropia*, on bark (lower trunk); Jun 2002, *Sipman 48034c* (B, INB). Las Cruces Biological Station. San Vito de Coto Brus; 82° 58' W, 8° 47' N, 1200 m; on ridge beyond Rio Java, on trunks and undergrowth of disturbed primary forest; Oct 2004, *Sipman 53258c* (B 60 0127363, INB), *53263* (B, INB).

Ocellularia maxima* (Hale) Lumbsch & Mangold, *comb. nov. (Fig. 24C)
MycoBank #800066

Thelotrema maximum Hale, Smithson. Contr. Bot. 38: 45 (1978); *Myriotrema maximum* (Hale) Hale, Mycotaxon 11: 134 (1980). Holotype. Panama, *Hale 43580* (US!).

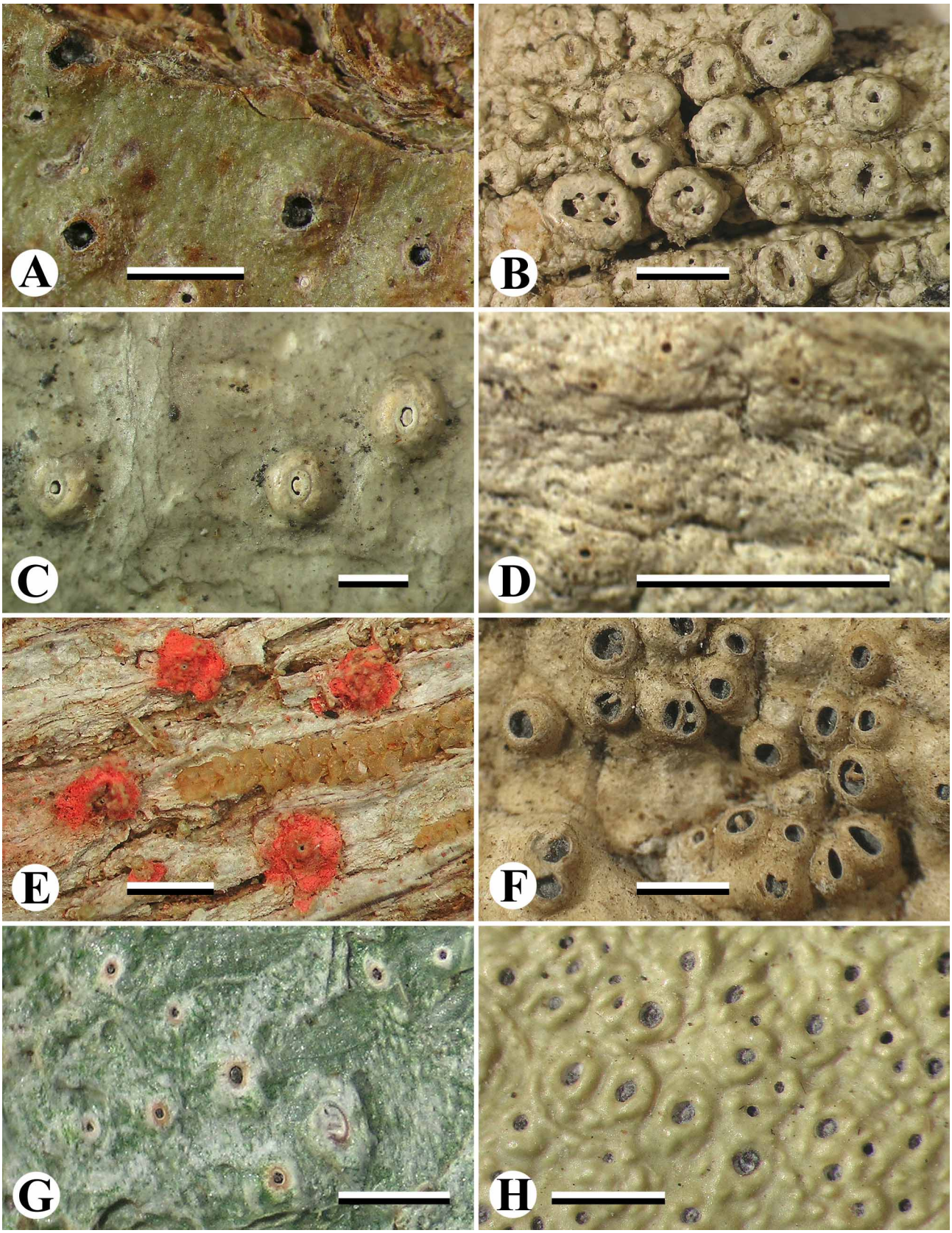

FIGURE 24. A. *Ocellularia landronii*. B. *Ocellularia mauritiana*. C. *Ocellularia maxima*. D. *Ocellularia minutula*. E. *Ocellularia mordenii*. F. *Ocellularia obturascens*. G. *Ocellularia papillata*. H. *Ocellularia perforata*. Scale = 1 mm.

Thallus light grey-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 1.5–2 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, filled by brown-black, white-pruinose columella; margin annulate, grey, laterally covered by thick thalline layer. Columella partly present, irregular, upper half carbonized. Excipulum prosoplectenchymatous, apically carbonized; periphysoids absent. Hymenium 200–250 µm high, clear; paraphyses unbranched. Ascospores 1–2/ascus, richly muriform, 100–170 × 30–40 µm, ellipsoid, with slightly thickened septa and rectangular lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—*Ocellularia maxima* belongs in a group of species with robust, columellate, carbonized apothecia, large muriform ascospores, and psoromic acid. Among these, including *O. interposita* (see above) and *O. postposita* (see below), the species is distinguished by its rather smooth thallus with prosoplectenchymatous cortex, the annulate apothecial margin, the irregular columella which is mostly carbonized in its upper half, and the only apically carbonized excipulum. *Ocellularia postposita* appears to differ only in having much smaller apothecia, whereas *O. interposita* has a different thallus structure and non-annulate apothecia.

Specimens examined:—COSTA RICA. San José: Cordillera de Talamanca, Interamerican Highway near El Empalme, S side of the highway to San Pablo; 9° 13' N, 83° 37' W, 2200 m; lower mountain rainforest; Dec 1978, *Kalb & Plöbst 31733*, *31735*, *38918* (hb. Kalb).

***Ocellularia minutula* Hale** (Fig. 24D)

Ocellularia minutula Hale, Smithson. Contr. Bot. 38: 24 (1978); *Myriotrema minutulum* (Hale) Hale, Mycotaxon 11: 134 (1980). Holotype. Panama, *Hale 43341* (US!).

Thallus light grey-green, smooth to uneven-verrucose, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.1–0.3 mm diam.; disc covered by narrow, 0.1 mm wide pore, filled by brown-black, white-pruinose columella; margin entire, pale brown, laterally covered by thalline layer. Columella partly present, simple, apically dark brown. Excipulum prosoplectenchymatous, brown; periphysoids absent. Hymenium 100–150 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–5-septate, 15–30 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ dark violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This species appears to be related to *Ocellularia terebrata* from which it differs in the rather light, almost verrucose thallus and the small, uncarbonized apothecia with inconspicuous columella. The columella is in fact easily overlooked and was not mentioned by Hale (1978) in its original description but is present in at least some of the apothecia.

Specimens examined:—*Ocellularia minutula* has not yet been found in Costa Rica but is known from Panama (Hale 1978).

***Ocellularia mordenii* Hale** (Fig. 24E)

Ocellularia mordenii Hale, Smithson. Contr. Bot. 16: 22 (1974). Holotype. Lesser Antilles (Dominica), *Hale 37765* (US!).

Thallus light grey-olive, verrucose, with loose cortex; medulla cinnabar-red; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.5–1 mm diam.; disc covered by narrow, 0.1 mm wide pore, invisible; margin entire, brown-black, white-pruinose, laterally

covered by thalline layer. Columella absent. Excipulum prosoplectenchymatous, upper half carbonized; periphysoids absent. Hymenium 200–250 µm high, clear; paraphyses unbranched. Ascospores 1–2/ascus, 21–39-septate, 100–200 × 15–25 µm, oblong, with thick septa and lens-shaped lumina, colorless, I+ dark violet-blue (amyloid). Secondary chemistry: medulla with cinnabar-red (K+ purple) anthraquinone; otherwise no substances detected by TLC.

Remarks:—*Ocellularia mordenii* is characterized by the cinnabar-red medulla but otherwise lacking secondary substances, the medium-sized ecolumellate, carbonized apothecia, and the large multiseptate ascospores. Most similar is *O. xanthostroma* (see below), which has an orange medulla and larger apothecia with slightly smaller, more numerous ascospores per ascus.

Specimens examined:—COSTA RICA. Puntarenas: Corcovado National Park, Los Patos Section, Los Patos Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, access trail to station and first, hilly part (5 km) of trail to Sirena; 83° 29' W, 8° 34' N, 100–300 m; lowland rain forest zone, closed primary forest, on bark (lower trunk), partially shaded; Apr 2003, *Grube 11442* (GZU, INB).

***Ocellularia obturascens* (Nyl.) Hale** (Fig. 24F)

Ocellularia obturascens (Nyl.) Hale, Sched. Lich. Amer. Exs., Fasc. 5, no. 110 (1970); Egan, Bryologist 90: 164 (1987); *Thelotrema bahianum* var. *obturascens* Nyl., Acta Soc. Sci. Fenn. 7: 453 (1863). Holotype. Colombia, *Lindig 719* (H-NYL!).

Thelotrema epitrypum f. *simplicius* Nyl., Acta Soc. Sci. Fenn. 7: 495 (1863). Holotype. Colombia, *Lindig 2580* (H-NYL!; isotype: BM!).

Thelotrema rudius Vain., Ann. Acad. Sci. Fenn., Ser. A, 6(7): 135 (1915); *Ocellularia rudius* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 639 (1923). Holotype. Lesser Antilles (Guadeloupe), *Duss 152* (TUR-VAIN 26790!).

Thallus grey-olive-yellow, minutely grainy, with loose cortex; photobiont layer and medulla with columnar clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.4–1 mm diam.; disc partially covered by 0.2–0.6 mm wide pore, partly filled by brown-black, white-pruinose (pseudo-)columella; margin entire, brown, laterally covered by thick thalline layer. (Pseudo-)columella partly present, irregular-reticulate, brown. Excipulum prosoplectenchymatous, apically brown; periphysoids absent. Hymenium 100–120 µm high, clear; paraphyses unbranched, thick. Ascospores 8/ascus, muriform, 15–25 × 10–15 µm, ellipsoid, with thick septa and rounded lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: protocetraric and virensic acids.

Remarks:—*Ocellularia obturascens* is very similar to *O. bahiana* except for the absence of a (pseudo-)columella. The two species were considered conspecific by Harris (1990), but the distribution of specimens with and without (pseudo-)columella is distinctive: all northeastern Brazilian collections (Cáceres 2007) lack a columella whereas for example all collections from Florida (Lücking *et al.* 2011) are columellate. Molecular data also show that material identified as *O. bahiana* from Australia (Mangold *et al.* 2009) is different from *O. obturascens* in Florida (Rivas Plata *et al.* 2012b).

Specimens examined:—COSTA RICA. Guanacaste: Upper portion of cañon of Río San José; 460–480 m; Feb 1930; *Dodge & Thomas 7828* (FH). Puntarenas: Near Las Cruces Botanical Garden (Coto Brus), 4 km SSE of San Vito; 82° 57' W, 8° 43' N, 1300 m; premontane rain forest zone, shady montane rain forest on slope near waterfall of Rio Jaba, on trunk; Jan 1979, *Sipman 11998* (B, U).

***Ocellularia papillata* (Leight.) Zahlbr.** (Fig. 24G)

Ocellularia papillata (Leight.) Zahlbr., Cat. Lich. Univ. 2: 597 (1923); *Thelotrema papillatum* Leight., Trans. Linn. Soc. London 27: 169 (1869). Lectotype (Hale 1974: 24): Sri Lanka, *Thwaithes 129* (BM!; isolectotypes: G!, H-NYL 3854!, S!, UPS!, W!).

Myriotrema rongklaense Homchantara & Coppins, Lichenologist 34: 116 (2002). Holotype. Thailand, *Wongshewarat et al.* 9497 (RAMK!).

Thelotrema cinereoglaucescens Vain., Ann. Acad. Sci. Fenn., Ser. A, 15(6): 189 (1921); *Ocellularia cinereoglaucescens* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 586 (1923); *Myriotrema cinereoglaucescens* (Vain.) Hale, Mycotaxon 11: 132 (1980). Lectotype (Hale 1981: 276). Philippines, *Elmer 14957* (TUR-VAIN 26875!; isolectotypes: BM, FH!, L!, W!).

Thallus light grey-green, smooth to uneven or white-papillose, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.4–0.7 mm diam.; disc covered by narrow, 0.1–0.15 mm wide pore, filled by brown-black, white-pruinose columella; margin entire, brown, laterally covered by thalline layer. Columella present, simple, dark brown. Excipulum prosoplectenchymatous, dark brown; periphysoids absent. Hymenium 80–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–5-septate, 20–35 × 6–10 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Ocellularia papillata* forms the center of a group of species that also includes *O. perforata*, *O. terebrata*, and *O. thelotremoides* (see below), characterized by a thallus with prosoplectenchymatous cortex with internal splitting, small, immersed-erumpent apothecia, small ascospores, and variable chemistry but usually psoromic or protocetraric acid. Excipular and columella carbonization varies greatly in this group and often one can find specimens with pale excipulum but carbonized columella or viceversa. This variation has usually been accepted at the species level, and forms with different levels of carbonization have been included within *O. papillata*, for example. However, such variation is not known from other groups within the *Ocellularia-Myriotrema* clade and thus we postulate that these forms are specifically distinct and sometimes not even closely related. This is supported by molecular data (Rivas Plata *et al.* 2012b). Therefore, *O. papillata* is here accepted to include specimens with (dark) brown but not distinctly carbonized excipulum and columella. The white papillae on the thallus correspond to accumulations of calcium oxalate crystals. They may be flat or slightly raised, and are found similarly in *O. perforata*. The species was already reported from Costa Rica by Breuss (2001).

Specimens examined:—COSTA RICA. Limón: Hitoy Cerere Biological Reserve, Hitoy Cerere Biological Station (La Amistad Caribe Conservation Area), Talamanca Ridge, 125 km ESE of San José, 40 km S of Limón, near Pandora, trails through forest above station (Sendero Espavel and Sendero Tepesquintle); 83° 02' W, 9° 40' N, 150–300 m; lowland to lower montane rain forest zone, partly disturbed primary forest, on bark (lower trunk), partially shaded; March 2004, *Sipman 51617* (B, INB), *51619* (B, INB), *51632* (B, INB). Puntarenas: Corcovado National Park, Los Patos Section, Los Patos Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, access trail to station and first, hilly part (5 km) of trail to Sirena; 83° 29' W, 8° 34' N, 100–300 m; lowland rain forest zone, closed primary forest, on bark (lower trunk), semi-exposed; Apr 2003, *Buck 44076* (CR, NY). Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, round trail NW of station (Sendero Sirena and Sendero Guanacaste); 83° 35' W, 8° 29' N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (lower stem), partially shaded; Apr 2003, *Lücking 16234c* (F), *Sipman 51175a* (B, CR), *51175e* (B, CR); ibid., second part of trail from Los Patos to Sirena station; 83° 33' W, 8° 32' N, sea level; lowland rain forest zone, oldgrowth secondary forest and closed secondary vegetation, on bark (lower stem), semi-exposed; Apr 2003, *Sipman 51087* (B, INB), *51088c* (B, CR), *51088e* (B, CR), *51092a* (B, INB), *51092b* (B, CR), *51097d* (B, CR); ibid., beach south of station; 83° 36' W, 8° 28' N, sea level; lowland coastal rain forest zone, disturbed coastal forest and exposed trees along beach, on bark (lower stem), semi-exposed; Apr 2003, *Sipman 51143* (B, CR). Fila Cruces Ridge, surroundings of Las Cruces Tropical Botanical Garden, 4 km SSE of San Vito; 8° 43' N, 82° 58' W, 1550 m; in a premontane rainforest at a waterfall; Jan 1979, *Kalb & Plöbst 38920*, *38936* (hb. Kalb). Las Tablas Protection Zone, La Neblina Section (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km ENE of San Vito near Las Mellizas, access road to fincas; 82° 45' W, 8° 55' N, 1600

m; montane rain forest zone, disturbed primary forest, on bark (lower trunk), semi-exposed; Jun 2002, *Lücking 15129k* (F, INB). Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), fully shaded; Feb 1997, *Lücking 97-76* (F). Wilson Botanical Garden, Las Cruces Biological Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 190 km SE of San José, trail beyond botanical garden; 82° 58' W, 8° 47' N, 1200 m; montane rain forest zone, primary forest, on bark (lower trunk), fully shaded; Sep 2007, *Lücking 21073b* (F), *OTS course P7-MR* (F). Near Las Cruces Garden, c. 4 km SSE of San Vito; 82° 57' W, 8° 43' N, 1300 m; premontane rain forest zone, light montane rain forest on slope near Rio Java, on trunk; Jan 1979, *Sipman 12008* (U). Cordillera de Tilaran, Monteverde, near the cheese factory; 84° 49' W, 10° 18' N, 1450 m; premontane rain forest zone, forest relicts among pasturefields, on trunks; Jan 1979, *Sipman 12118* (U).

***Ocellularia perforata* (Leight.) Müll. Arg.** (Fig. 24H)

Ocellularia perforata (Leight.) Müll. Arg., Hedwigia 31: 284 (1892); *Thelotrema perforatum* Leight., Trans. Linn. Soc. London 25: 477 (1866). Lectotype (Hale 1974: 25). Brazil, *Spruce s.n.* (BM!: Spruce, Lichenes Amazonici et Andini 254; isolectotype: H-NYL 22557!).

Ocellularia rufocincta Müll. Arg., Bull. Soc. Bot. Belgique 32: 146 (1893). Holotype. Costa Rica, *Pittier 6107* (G!).

Thelotrema excavatum Vain., J. Bot. 34: 208 (1896); *Ocellularia excavata* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 590 (1923). Holotype. Lesser Antilles (St. Vincent), *Elliott 153* (TUR-VAIN 26881!; isotypes: BM!, FH!).

Thelotrema excavatum var. *impressulum* Vain., J. Bot. 34: 208 (1896); *Ocellularia excavata* var. *impressula* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 590 (1923). Holotype. Lesser Antilles (Dominica), *Elliott 169* (TUR-VAIN 26880!).

Ocellularia violacea var. *glauca* Räsänen, Suom. Elain-ja Kasvit. Seuran Van. Tiedon. Pöytäkirjat (Arch. Soc. Zool. Bot. Fenn. Vanamo) 3: 185 (1949). Holotype. Australia, *Wilson s.n.* (H-Räsänen!).

Myriotrema subminutum Homchantara & Coppins, *Lichenologist* 34: 117 (2002). Holotype. Thailand, *Wongshewarat et al. 9421-3* (RAMK!).

Myriotrema khaoyaianum Homchantara & Coppins, *Lichenologist* 34: 115 (2002). Holotype. Thailand, *Homchantara 9183* (RAMK!).

Thallus grey-olive, uneven to verrucose or white-papillose, with dense, paraplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.3–0.8 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, filled by brown, white-pruinose columella; margin entire, brown, laterally covered by thalline layer. Columella present, simple, apically dark brown. Excipulum prosoplectenchymatous, apically dark brown; periphysoids absent. Hymenium 100–130 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–9-septate, 20–35 × 8–10 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: protocetraric and virensic acids, sometimes also succinprotocetraric acid (surface UV–; medulla P+ orange-red; section K–).

Remarks:—*Ocellularia perforata* is like the closely related *O. papillata* (see above) a species complex, comprising forms with variable excipular and columella carbonization. We have accepted under *O. perforata* s.str. specimens with (dark) brown excipulum and columella, thus similar to *O. papillata*, but differing in the presence of the protocetraric acid chemosyndrome. Specimens with distinctly carbonized excipulum and/or columella have to be studied further, as they possibly represent separate taxa. Preliminary molecular data suggest that some of these forms are not even closely related (Rivas Plata *et al.* 2012b). The reported variation in ascospore size (with up to 50 µm) also suggests that there are several taxa involved, one now being separated as *O. cryptica* (see above). The specimen *Sipman 44335* agrees with typical *O. perforata* in most aspects but does not cluster with that species in a phylogenetic analysis (Rivas Plata *et al.* 2012b), suggesting another separate, cryptic species. The record of *O. bonplandii* Spreng. by Müller (1891) probably belongs to *O. perforata*. The species was reported from Costa Rica by Breuss (2000, 2001).

Specimens examined:—COSTA RICA. Alajuela: San Ramón Forest Reserve, near house at Río Lorencito, c. 5 km NE of Cerro Jabonal; 84° 37' W, 10° 13' N, 1000 m; humid, mossy forest with many ferns on mountain ridge, on thin trunk in undergrowth; Nov 1988, *Sipman et al. 41965* (B, CR). Guanacaste: Palo Verde National Park, Palo Verde Station (Tempisque Conservation Area), Río Tempisque Bassin, 130 km WNW of San José and 30 km SSW of Bagaces, lower parts of Guayacan trail; 85° 21' W, 10° 21' N, 10–50 m; lowland to lower montane moist forest zone, disturbed primary forest remnants and open secondary forest, on bark (lower stem), semi-exposed; Mar 2003, *Sipman 50983a* (B, INB). Limón: Caribbean coast, Cahuita; 82° 50' W, 9° 44' N, 50 m; cacao plantation SW of the village, on *Theobroma* branches; Jan 1979, *Sipman 12286* (U). Hitoy Cerere Biological Reserve, Hitoy Cerere Biological Station (La Amistad Caribe Conservation Area), Talamanca Ridge, 125 km ESE of San José, 40 km S of Limón, near Pandora, trails through forest above station (Sendero Espavel and Sendero Tepesquintle); 83° 02' W, 9° 40' N, 150–300 m; lowland to lower montane rain forest zone, partly disturbed primary forest, on bark (lower trunk), partially shaded; Mar 2004, *Sipman 51629* (B, INB); ibid., on bark (liana), partially shaded; Mar 2004, *Sipman 51653* (B, INB). Puntarenas: Carara Biological Reserve, c. 15 km SSW of Orotina; 84° 37' W, 9° 47' N, 50 m; disturbed primary, c. 40 m tall forest, along trail near warden's house, on thin trunk in undergrowth; Nov 1988, *Sipman & Döbbeler 42222* (B, CR). Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, beach south of station; 83° 36' W, 8° 28' N, sea level; lowland coastal rain forest zone, disturbed coastal forest and exposed trees along beach, on bark (lower stem), semi-exposed; Apr 2003, *Sipman 51156b* (B, INB); ibid., round trail NW of station (Sendero Sirena and Sendero Guanacaste); 83° 35' W, 8° 29' N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (lower stem), partially shaded; Apr 2003, *Sipman 51170d* (B, INB). Fila Cruces Ridge, surroundings of Las Cruces Tropical Botanical Garden, 4 km SSE of San Vito; 8° 43' N, 82° 58' W, 1550 m; in a premontane rainforest at a waterfall; Jan 1979, *Kalb & Plöbst 31825*, *31826*, *38926* (hb. Kalb). Las Tablas Protection Zone, Cedro Ridge, Las Alturas Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km NE of San Vito near Alturas, surroundings of station and trail into forest; 82° 50' W, 8° 57' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower stem), partially shaded; Jun 2002, *Lücking 15076d* (INB). Las Cruces Biological Station, San Vito de Coto Brus; 82° 58' W, 8° 47' N, 1200 m; on ridge beyond Río Java, on trunks and undergrowth of disturbed primary forest; Oct 2004, *Sipman 53258b* (B 60 0127360, INBio). Near Las Cruces Garden, c. 4 km SSE of San Vito; 82° 57' W, 8° 43' N, 1300 m; shady montane rain forest on slope near waterfall of Río Java, on trunk; Jan 1979, *Sipman 11985* (U), *12009* (U). Manuel Antonio National Park, near Quepos; 84° 09' W, 9° 23' N, sea level; scattered trees around hotel at end station of bus line; Nov 1988, *Sipman 42312* (B, CR); ibid., primary forest close to the seashore; Nov 1988, *Sipman 42325* (B, CR), *42326* (B, CR), *42329* (B, CR). Monteverde, Cordillera de Tilaran, near the cheese factory; 84° 49' W, 10° 18' N, 1450 m; premontane rain forest zone, forest relicts among pasturefields, on trunks; Jan 1979, *Sipman 12114* (U), *12117* (U). San José: Cordillera de Talamanca, ca. 5 km W of Cerro de la Muerte, San Gerardo de Dota, along Quebrada Ojo de Agua; 83° 48' W, 9° 35' N, 2600 m; epiphyte; Mar 1985, *Sipman & Chaverri 20788* (B, CR). San Gerardo de Dota, Finca Chacón, near entrance of Sendero La Quebrada; 83° 48' W, 9° 33' N, 2800 m; mixed, light, primary *Quercus* forest on steep slope, on sapling; Nov 1999, *Sipman 44335* (B 60 0107620).

Ocellularia pluriporoides **Homchantara & Coppins** (Fig. 25A)

Ocellularia pluriporoides Homchantara & Coppins, Lichenologist 34: 127 (2002). Holotype. Thailand, *Wolseley & Aguirre-Hudson 5112* (BM!).

Thallus grey-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.6–0.9 mm diam.; disc

covered by narrow, 0.05–0.2 mm wide pore, filled by brown-black, white-pruinose columella; margin entire, pale brown, laterally covered by thalline layer. Columella present, simple to reticulate, apically carbonized. Excipulum prosoplectenchymatous, pale brown; periphysoids absent. Hymenium 100–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 7–13-septate, 30–50 × 7–10 µm, oblong, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—*Ocellularia pluriporoides* resembles *O. terebrata* (see below) but has a reticulate columella, an uncarbonized excipulum, and larger ascospores with more numerous septa. The Costa Rican material matches the type well. Also similar are *O. minutula* (see above) and *O. pluripora* Hale, both with simple columella (uncarbonized in the first) and smaller ascospores. *Ocellularia psorbarroensis* (see below) also has an irregular but uncarbonized columella and smaller ascospores than *O. pluriporoides*. The most similar species of *Stegobolus*, *S. anamorphus* (see below), has larger, prominent to sessile apothecia and distinctly smaller ascospores.

Specimens examined:—COSTA RICA. Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, second part of trail from Los Patos to Sirena station; 83° 33' W, 8° 32' N, sea level; lowland rain forest zone, oldgrowth secondary forest and closed secondary vegetation, on bark (lower trunk), partially shaded; Apr 2003, *Lücking 16359a* (INB).

***Ocellularia praestans* (Müll. Arg.) Hale** (Fig. 25B)

Ocellularia praestans (Müll. Arg.) Hale, Mycotaxon 11: 137 (1980); *Thelotrema praestans* Müll. Arg., J. Linn. Soc. London, Bot., 30: 453 (1895). Lectotype (Hale 1974: 36). Lesser Antilles (St. Vincent), *Elliott 246 p.p.* (BM!).
Thelotrema elliottii Vain., J. Bot. 34: 207 (1896). Holotype. Lesser Antilles (St. Vincent), *Elliott 246 p.p.* (TUR-VAIN 26821!; isotype: BM!).

Thallus grey-green, papillose, with dense, paraplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 1–2 mm diam.; disc covered by narrow, 0.15–0.3 mm wide pore, filled by brown-black, white-pruinose columella; margin entire, white-grey, laterally covered by thick thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 300–400 µm high, clear; paraphyses unbranched. Ascospores 1–2/ascus, richly muriform, 150–300 × 30–40 µm, oblong, with slightly thickened septa and rectangular lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: subpsoromic acid.

Remarks:—*Ocellularia praestans* belongs in a group of species with large, robust, carbonized and columellate apothecia and large muriform ascospores. Most unusual about this species is the chemistry, usually given as 'praestans' unknown (Hale 1974, 1978) but subsequently identified as subpsoromic acid (Cáceres 2007). The latter usually accompanies psoromic acid but is rarely found as single major compound. The most similar species in this group with psoromic acid as major compound would be *O. interposita* (see above), which however has a different thallus structure and color. *Ocellularia praestans* should not be confused with *O. piperis* (Vain.) Aptroot, which agrees in most characters but has hypoprotocetraric acid as major compound. The latter was identified as *O.* aff. *praestans* in Cáceres (2007). *Ocellularia praestans* seems to prefer mid-elevation rain forests.

Specimens examined:—COSTA RICA. Cartago: La Chonta; 83° 56' W, 09° 42' N, 2400–2500 m; Jul 2007, *Chaves 2782* (INB). Puntarenas: Monteverde, Cordillera de Tilaran, near the cheese factory; 84° 49' W, 10° 18' N, 1450 m; premontane rain forest zone, forest relicts among pasturefields, on trunks; Jan 1979, *Sipman 12116* (U). Guanacaste: Cacao Biological Station (Guanacaste Conservation Area); 85° 28' W, 10° 56' N, 1000 m; epiphyte in humid primary montane forest near the station; Jun 1995, *Sipman 37290* (B, CR). Volcán Tenorio National Park, 15 km NNW of Tilarán, Alto Masis; 85° 00' W, 10° 36' N, 850–900 m; on tree in disturbed forest near Tierras Morenas; Mar 2004, *Aptroot 60638* (hb. Aptroot).

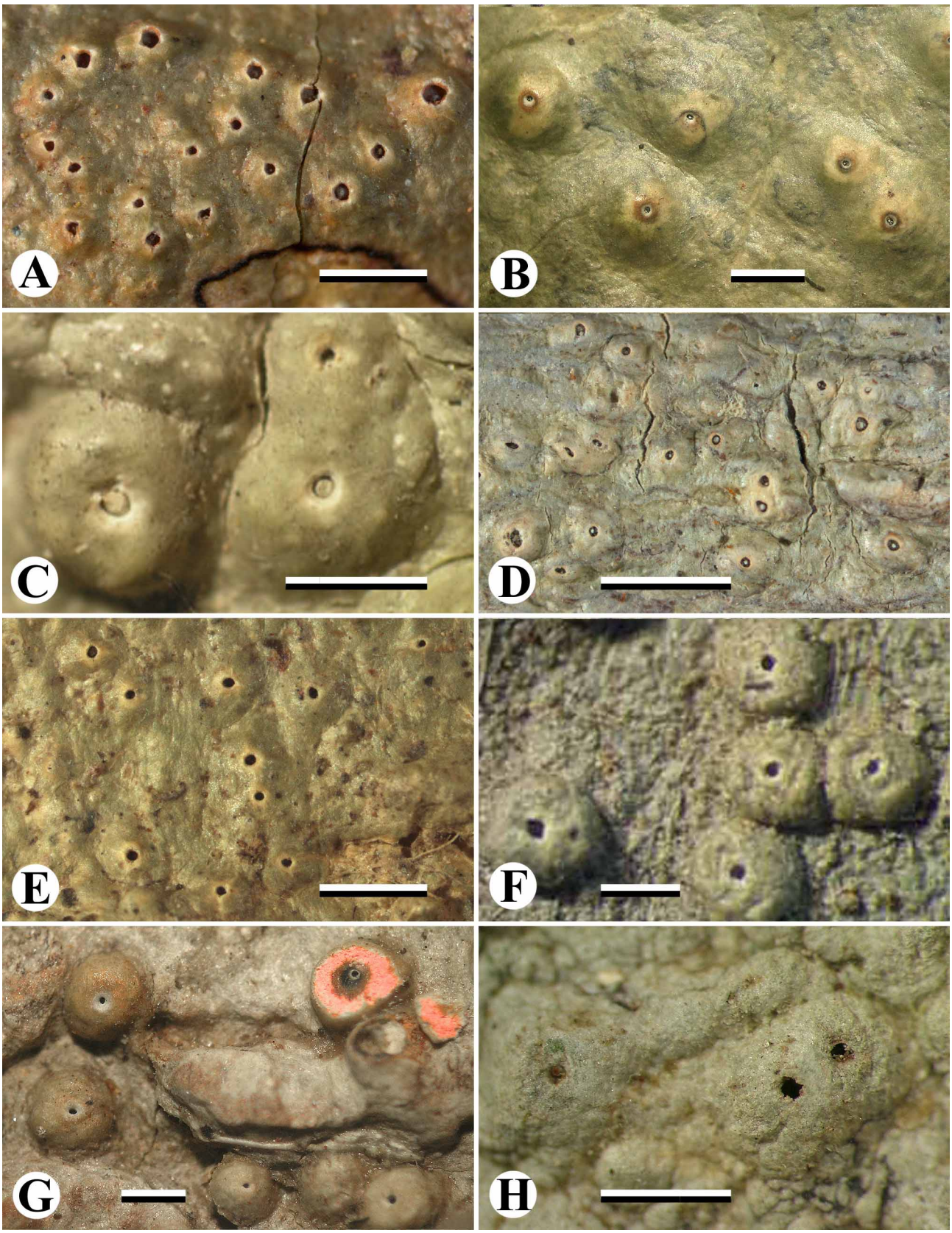

FIGURE 25. A. *Ocellularia pluriporoides*. B. *Ocellularia praestans*. C. *Ocellularia praestantoides*. D. *Ocellularia pseudopyrenuloides*. E. *Ocellularia psorbarroensis*. F. *Ocellularia rhabdospora*. G. *Ocellularia rhodostroma*. H. *Ocellularia ripleyi*. Scale = 1 mm.

Ocellularia praestantoides **Sipman, *spec. nov.*** (Fig. 25C)
MycoBank #800092

Differing from *Ocellularia praestans* in the presence of protocetraric acid and the smaller ascospores.

Holotype:—COSTA RICA. Puntarenas: Manuel Antonio National Park, near Quepos; 9° 23' N, 84° 09' W, sea level; scattered trees around hotel at end station of bus line; Nov 1988, *Sipman 42307* (B; isotype: CR).

Thallus grey-green, verrucose, with dense, paraplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 1–1.8 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, filled by brown-black, white-pruinose columella; margin entire, white-grey, laterally covered by thalline payer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 200–300 µm high, clear; paraphyses unbranched. Ascospores 1–2/ascus, richly muriform, 80–120 × 25–35 µm, ellipsoid, with slightly thickened septa and rectangular lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: protocetraric and virensic acids.

Remarks:—This is a new species in the *Ocellularia praestans* group characterized by protocetraric acid as major compound and virensic as accessory substance. There is no other species with columellate, carbonized apothecia and large muriform ascospores with this chemistry. Three other species with robust apothecia, large muriform ascospores, and protocetraric acid as major or accessory compound, viz. *O. kansriae* Homchantara & Coppins, *O. khasianum* Patw. & Nagarkar, and *O. microstoma* (Müll. Arg.) Mangold, all lack a columella, and the latter species also differs in the dark brown instead of carbonized excipulum and fumarprotocetraric acid as major compound. Interestingly, all collections of the new species originate from seasonally dry evergreen forest in the central and northwestern parts of Costa Rica.

Additional specimens examined (paratypes):—COSTA RICA. Guanacaste: Monte Alto Forest Reserve, Monte Alto Biological Station (Tempisque Conservation Area), Nicoya Peninsula, 150 km W of San José, 10 km SSE of Nicoya, near Hojancha, main trails and access road through reserve near station (Sendero Jardín de Orquideas, Sendero Ceiba, Sendero Shannon-Ward); 85° 24' W, 10° 02' N, 450–550 m; lowland to lower montane moist forest zone, disturbed primary and oldgrowth secondary forest, on bark (lower trunk), exposed; Mar 2004, *Sipman 52016* (B, INB-4063099). Puntarenas: Manuel Antonio National Park, near Quepos; 84° 09' W, 9° 23' N, sea level; scattered trees around hotel at end station of bus line; Nov 1988, *Sipman 42308* (B, CR), *42315* (B, CR); ibid., primary forest close to the seashore; Nov 1988, *Sipman 42328* (B, CR).

Ocellularia pseudopyrenuloides **Lücking, *spec. nov.*** (Fig. 25D)
MycoBank #800093

Differing from *Ocellularia pyrenuloides* in the uncarbonized apothecia and the presence of psoromic acid.

Holotype:—COSTA RICA. Heredia: La Selva Protection Zone, La Selva Biological Station (Cordillera Volcánica Central Conservation Area), Volcánica Central Ridge, 55 km N of San Jose, trail along forest margin (SHO trail); 84° 03' W, 10° 26' N, 50 m; lowland rain forest zone, closed primary forest, on bark (branch, fallen), semi-exposed; Jan 1997, *Lücking 97-21* (F).

Thallus white-grey, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.3–0.5 mm diam.; disc partially covered by narrow, 0.1–0.2 mm wide pore, filled by white columella; margin white, laterally covered by thalline layer. Columella present, simple, colorless. Excipulum prosoplectenchymatous, brown; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–5-septate, 15–20 × 5–6 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This is yet another new species with small, columellate apothecia, small, transversely septate ascospores, and psoromic acid. Like the newly described *O. albobullata* and *O. antillensis* (see above), it has a white-grey rather than green-grey thallus (the latter being characteristic for species with psoromic acid). What sets this species apart are the small, uncarbonized apothecia with regular and distinct, but completely colorless columella. A colorless (pseudo)columella is found in *O. albobullata* and *O. psorbarroensis* (see below), but both have much larger apothecia and the (pseudo)columella is irregular; in addition, *O. albobullata* features a bullate thallus, whereas in *O. psorbarroensis* the thallus is green-grey. *Ocellularia minutula* (see above) is probably closely related, but features an apically dark brown columella and the apothecia have a narrower pore. The epithet of the new species refers to the fact that it closely resembles *O. pyrenuloides* (see below) externally, but the latter has carbonized apothecia and stictic acid as major secondary substance.

Ocellularia psorbarroensis* Sipman, *spec. nov. (Fig. 25E)
MycoBank #800094

Differing from *Ocellularia barroensis* in the presence of psoromic acid.

Holotype:—COSTA RICA. Puntarenas: Corcovado National Park (Osa Conservation Area), Sirena Biological Station, upper part of trail from Los Patos to Sirena station; 83° 31' W, 8° 33' N, 100 m; disturbed primary lowland forest on ridge, on thin trunk; Apr 2003, *Sipman 51088h* (B; isotype: CR).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.8–1.2 mm diam.; disc covered by narrow, 0.1–0.3 mm wide pore; margin entire, grey-brown, white-pruinose, laterally covered by thalline margin. Pseudocolumella present, irregular, white. Excipulum prosoplectenchymatous, brown; periphysoids absent. Hymenium 100–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–7-septate, 20–25 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This new species is morphologically reminescent of *Ocellularia barroensis* and *O. mauritiana* (see above) and differs chiefly in its chemistry, the latter species having either no substances or protocetraric acid. *Ocellularia terebrata* (see below) agrees in chemistry but has carbonized apothecia.

Additional specimen examined (paratype):—COSTA RICA. Puntarenas: Monte Verde, Cordillera de Tilaran, ca. 20 km E of Juntas; Jan 1979, *Filson 16387* (MEL).

***Ocellularia rhabdospora* (Nyl.) Redinger** (Fig. 25F)

Ocellularia rhabdospora (Nyl.) Redinger, Arkiv Bot. 28A(8): 26 (1936); *Ascidium rhabdosporum* Nyl., Ann. Sci. Nat. Bot., Ser. 5, 7: 320 (1867). Lectotype (Hale 1978: 29). Colombia, *Lindig s.n.* (H-NYL 22432!; isolectotype: BM!).

Thallus grey-olive, verrucose, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 1–2 mm diam.; disc covered by narrow, 0.2–0.3 mm wide pore, filled by brown-black, white-pruinose columella; margin entire, yellowish white, laterally covered by thalline layer. Columella present, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 200–250 µm high, clear; paraphyses unbranched. Ascospores 1–2/ascus, 15–19-septate, 120–160 × 10–12 µm, cylindrical, with thick septa and lens-shaped lumina, colorless, I+ dark violet-blue (amyloid). Secondary chemistry: cinchonarum unknowns.

Remarks:—*Ocellularia rhabdospora* is close to the type species of the genus, *O. cavata* (see above), and differs from this and other species in this group by the lack of a medullary pigment, in combination with the comparatively large ascospores.

Specimens examined:—The species is not yet known from Costa Rica, but has been reported from Panama (Hale 1978).

***Ocellularia rhodostroma* (Mont.) Zahlbr.** (Fig. 25G)

Ocellularia rhodostroma (Mont.) Zahlbr., Cat. Lich. Univ. 2: 600 (1923); *Ascidium rhodostroma* Mont., Ann. Sci. Nat. Bot., Ser. 3, 16: 75 (1851). Lectotype (Hale 1974: 25). French Guiana, *Leprieur 1334* (PC!).

Thallus grey-olive, smooth to uneven, with dense, paraplectenchymatous cortex; medulla pink; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 1–2 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, invisible; margin annulate, grey, laterally covered by thalline layer. Columella absent. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 250–400 µm high, clear; paraphyses unbranched. Ascospores 1–2/ascus, 19–35-septate, 150–270 × 20–40 µm, oblong-ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids, medulla with pink (K+ yellow then aeruginous) pigment.

Remarks:—This common species is easily recognized by the pink medulla, the robust, carbonized apothecia lacking a columella, the large multiseptate ascospores and hypoprotocetraric acid as major compound besides the pigment. Most closely related is *O. americana* Hale, which shares the pink medullary pigment and multiseptate ascospores but has columellate apothecia and the unusual substance gyrophoric acid. The species was reported from Costa Rica by Breuss (2000).

Specimens examined:—COSTA RICA. Alajuela: Alto de Mondongo de San Ramón; 800 m; Jan 1930; *Brenes 299* (FH; as *Phaeotrema domingense* (Fée) Müll. Arg.). San Ramón Forest Reserve, near house at Río Lorencito, c. 5 km NE of Cerro Jabonal; 84° 37' W, 10° 13' N, 1000 m; humid, mossy forest with many ferns on mountain ridge, on thin trunk in undergrowth; Nov 1988, *Sipman et al. 41955* (B, CR), *41956* (B, CR), *41960* (B, CR), *41973* (B, CR), *41988* (B, CR). Volcán Tenorio National Park, Pilón Biological Station (Arenal-Tempisque Conservation Area), Tilarán Ridge, 140 km NW of San José, 25 km NNW of Tilarán, near Bijagua, access road to station and river; 84° 59' W, 10° 43' N, 700 m; lower montane cloud forest zone, exposed trees and fence posts along pasture, on bark (lower trunk), exposed; Mar 2004, *Sipman 51780* (B, INB); ibid., main trail through forest to crater; 84° 59' W, 10° 43' N, 700–900 m; lower montane cloud forest zone, partly disturbed primary forest, on bark (branch, fallen), exposed; Mar 2004, *Sipman 51912* (B, INB). Cartago: Chirripó National Park, trail from Base Crestones to San Gerardo; 9° 29' N, 83° 29' W, 2600 m; disturbed primary mossy mountain forest, on base of *Quercus* trunk along trail; 19 Mar 2000, *Sipman & Umaña 46561* (B, INB). Guanacaste: Cacao Biological Station (Guanacaste Conservation area); 85° 28' W, 10° 56' N, 1000 m; epiphyte in humid primary montane forest near the station; Jun 1995, *Sipman 37287* (B, CR), *37289* (B, CR). Volcán Tenorio National Park, Alto Masis Section (Arenal-Tilarán Conservation Area), Tilarán Ridge, 125 km NW of San José, 15 km NNW of Tilarán, near Tierras Morenas, surroundings of station; 85° 00' W, 10° 37' N, 950–1000 m; lower montane elfin cloud forest zone, disturbed low elfin forest and secondary vegetation, on bark (lower trunk), semi-exposed; Mar 2004, *Will-Wolf 12786a* (CR, INB, USJ, WIS), *12786b* (CR, INB, USJ, WIS). Limón: Braulio Carrillo National Park, Quebrada Gonzales Section (Cordillera Volcánica Central Conservation Area), Volcánica Central Ridge, 30 km NNW of San José, trail above station (Sendero El Ceibo); 83° 56' W, 10° 10' N, 500 m; lower montane rain forest zone, primary forest, on bark (lower trunk), partially shaded; Mar 2003, *Buck 44009* (INB, NY). Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, first part of trail from Sirena to Los Patos Station; 83° 35' W, 8° 30' N, sea level; lowland rain forest zone, primary forest remnants and closed secondary forest, on bark (lower

trunk), semi-exposed; Apr 2003, *Buck 44095* (INB, NY). Fila Cruces Ridge, surroundings of Las Cruces Tropical Botanical Garden, 4 km SSE of San Vito; 8° 43' N, 82° 58' W, 1550 m; in a premontane rainforest at a waterfall; Jan 1979, *Kalb & Plöbst 38944* (hb. Kalb). La Amistad International Park, Altamira Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 20 km N of San Vito near Finca Colorado, interpretative trail (Sendero Gigantes) behind station; 83° 00' W, 9° 02' N, 1500–1600 m; montane rain forest zone, disturbed primary forest and secondary vegetation dominated by *Cecropia*, on bark (lower trunk), partially shaded; Jun 2002, *Sipman 48014* (B, INB), 48032a (B, F, INB). Las Cruces Biological Station, San Vito de Coto Brus; 82° 58' W, 8° 47' N, 1200 m; on ridge beyond Río Java, on trunks and undergrowth of disturbed primary forest; Oct 2004, *Sipman 53264* (B, INBio). Las Tablas Protection Zone, Cedro Ridge, Las Alturas Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km NE of San Vito near Alturas, surroundings of station and trail into forest; 82° 50' W, 8° 57' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower trunk), fully shaded; Jun 2002, *Lücking 15078c* (INB); ibid., semi-exposed; Jun 2002, *Sipman 47820c* (B, INB), *47820e* (B, INB). Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), partially shaded; Feb 1997, Lücking 97-120a (F). San José: Cordillera de Talamanca, ca. 5 km W of Cerro de la Muerte, San Gerardo de Dota, along Quebrada Ojo de Agua; 83° 48' W, 9° 35' N, 2600 m; epiphyte; Mar 1985, *Sipman & Chaverri 20804* (B, CR).

***Ocellularia ripleyi* Hale** (Fig. 25H)

Ocellularia ripleyi Hale, Phytologia 27: 493 (1974). Holotype. Panama, *Hale 38664* (US!).

Thallus light grey-green, verrucose, with dense, paraplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 1–1.5 mm diam.; disc covered by narrow, 0.2–0.3 mm wide pore, filled by brown-black, white-pruinose columella; margin entire, yellow-white, laterally covered by thalline layer. Columella present, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 300–400 µm high, clear; paraphyses unbranched. Ascospores 1–2/ascus, 15–25-septate, 80–200 × 12–15 µm, cylindrical, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—*Ocellularia ripley* is recognized by the combination of robust, columellate, carbonized apothecia, large multiseptate ascospores, and psoromic acid. The only other species with that combination of characters is *O. canariana* Patw., Sethy & Nagarkar, but that species has a prosoplectenchymatous cortex, apothecia with a wider pore and irregular columella, and 8 ascospores per ascus. Morphologically similar is *O. dolichotata* (see above), but that species has ascospores twice as wide and lacks secondary substances.

Specimens examined:—COSTA RICA. Limón: Hitoy Cerere Biological Reserve, Hitoy Cerere Biological Station (La Amistad Caribe Conservation Area), Talamanca Ridge, 125 km ESE of San José, 40 km S of Limón, near Pandora, trail adjacent to access road before station; 83° 02' W, 9° 40' N, 150–200 m; lowland to lower montane rain forest zone, disturbed primary and oldgrowth secondary forest, on bark (lower trunk), semi-exposed; Mar 2004, *Aptroot 60188* (BR, INB), *Lücking 17047a* (F). Puntarenas: Finca Quebrada Bonita-Garabú, La Fila; 83° 35' W, 9° 34' N, 0–100 m; Nov 2008, *Chaves 3325* (INB).

Ocellularia subcarassensis* Sipman & Lücking, *spec. nov. (Fig. 26A)
MycoBank #800095

Differing from *Ocellularia carassensis* in the uncarbonized excipulum and smaller ascospores.

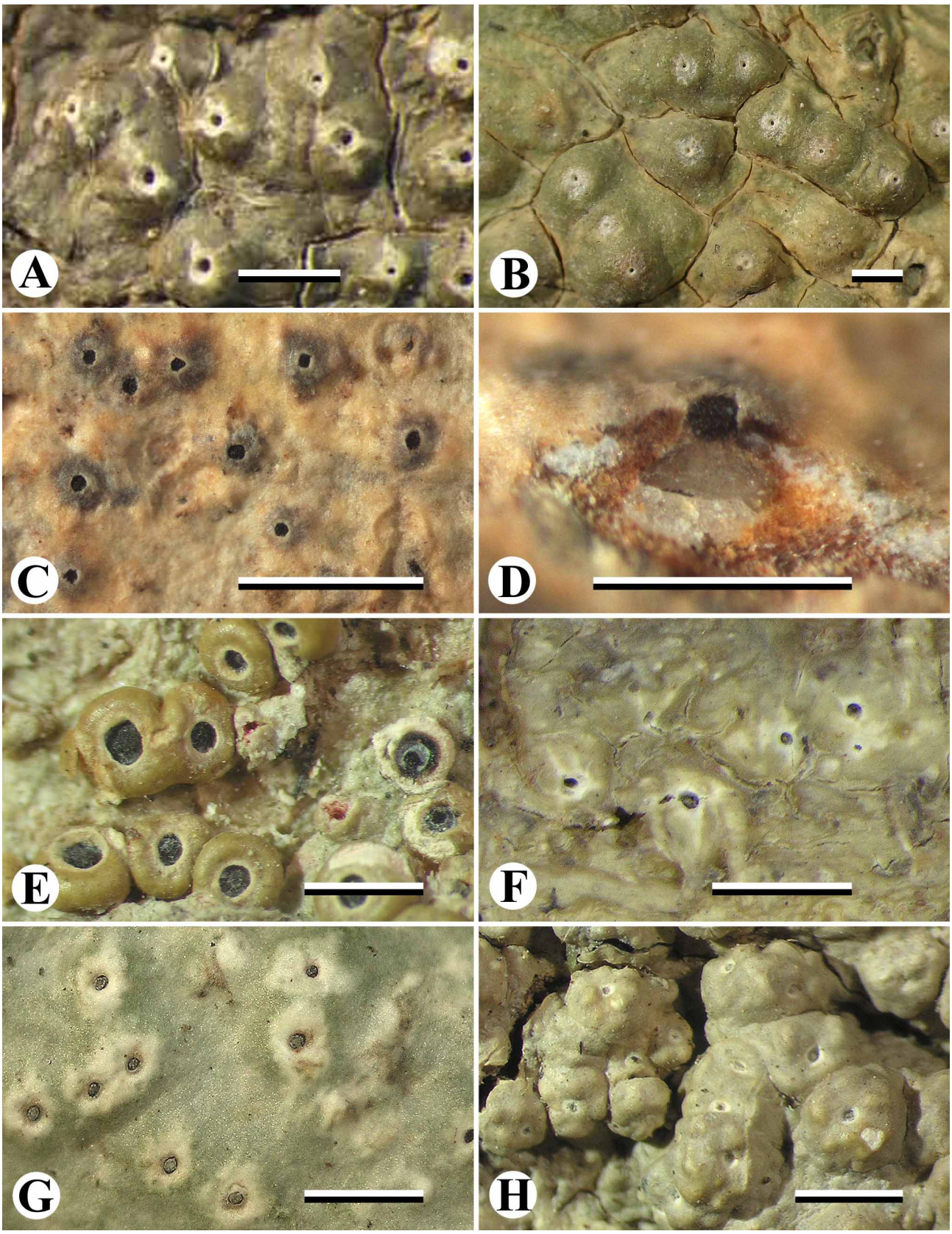

FIGURE 26. A. *Ocellularia subcarassensis*. B. *Ocellularia subpraestans*. C–D. *Ocellularia subpyrenuloides*. E. *Ocellularia supergracilis*. F. *Ocellularia tacarcunae*. G. *Ocellularia terebrata*. H. *Ocellularia terrabensis*. Scale = 1 mm except D = 0.5 mm.

Holotype:—EL SALVADOR. Santa Ana: Metapán, Montecristo National Park, Cerro Miramundo; 89° 23' W, 14° 26' N, 2400 m; scrub on exposed ridge; Nov 1993, *Sipman et al. 37559* (B).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with small clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.6–1 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, invisible; margin entire, white-grey, laterally covered by thalline layer. Columella absent. Excipulum prosoplectenchymatous, brown; periphysoids absent. Hymenium 150–180 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, muriform, 30–40 × 12–15 µm, fusiform, with slightly thickened septa and rectangular lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This new species is reminescent of material from Dominica identified as *Thelotrema carassense* Vain. by Hale (1974). The latter is combined in *Ocellularia* below. However, *O. carassensis* has distinctly larger ascospores (60–120 × 20–35 µm) in numbers of 2–4/ascus and a distinctly carbonized excipulum, and therefore the material from El Salvador is here described as new species. *Ocellularia conformis* (see above) is the columellate, carbonized counterpart to *O. subcarassensis*. Also similar is *O. umbilicata* (see below), which agrees in all aspects with *O. subcarassensis* except for the transversely septate ascospores. The aforementioned Dominica specimens deviate because they are stated to be weakly carbonized in the upper part of the excipulum (Hale 1974).

Ocellularia carassensis* (Vain.) Sipman**, ***comb. nov. [MycoBank #800226; *Thelotrema carassense* Vain., Étud. Lich. Brésil 2: 79 (1890). Lectotype (Hale 1974: 34). Brazil, *Vainio s.n.* (TUR-VAIN 26837!; Vainio, Lich. Bras. Exsicc. 1523; isolectotypes: BM!, FH!, PC!). Syn.: *Thelotrema minarum* Vain., Étud. Lich. Brésil 2: 79 (1890). Holotype. Brazil, *Vainio s.n.* (TUR-VAIN 26835!; Vainio, Lich. Bras. Exsicc. 1397; isotypes: BM!, FH!, UPS!)].

***Ocellularia subpraestans* (Hale) Hale** (Fig. 26B)

Ocellularia subpraestans (Hale) Hale, Mycotaxon 11: 138 (1980); *Thelotrema subpraestans* Hale, Phytologia 27: 497 (1974). Holotype. Panama, *Hale 38525* (US!).

Thallus light grey-green, smooth to uneven, with dense, paraplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 1.5–2.5 mm diam.; disc covered by narrow, 0.1 mm wide pore, filled by brown-black, white-pruinose columella; margin entire, yellowish white. Columella present, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 500–700 µm high, clear; paraphyses unbranched. Ascospores single, richly muriform, 300–700(–880) × 30–50(–65) µm, oblong-fusiform, with slightly thickened septa and rectangular lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: stictic, constictic, and hypostictic acids.

Remarks:—This species is quite unusual within *Ocellularia* s.lat. in producing stictic acid, a substance much more common in the *Chapsa-Leucodecton-Thelotrema* clade (Rivas Plata *et al.* 2010a). Another striking feature is the very large ascospores, two to three times as large as in any other species of the family. These are the longest, and among the largest, fungal spores known, surpassed in volume only by some species of *Pertusaria* (Ingold 2001; Sweetwood *et al.* 2012). In his original description, Hale (1978) gave the ascospores as up to 300 µm, but restudy of the type material showed that they are about twice as large (up to 650 µm). This coincides with our measurements of Costa Rican material, whereas in other material from Panama, ascospores up to 880 × 65 µm where found (Sweetwood *et al.* 2012). *Ocellularia subpraestans* appears to be strictly confined to lowland rain forest close to sea level.

Specimens examined:—COSTA RICA. Alajuela: San Pedro de San Ramón; 700 m; Feb 1930; *Brenes 296* (FH; as *Thelotrema depressum* Mont.). Limón: Caribbean coast, S of Cahuita; 82° 50' W, 9° 44' N, sea level; *Cocos* trunks in orchard immediately S of the village; Jan 1979, *Sipman 12297* (B). Hitoy Cerere Biological Reserve, Hitoy Cerere Biological Station (La Amistad Caribe Conservation Area), Talamanca

Ridge, 125 km ESE of San José, 40 km S of Limón, near Pandora, trail adjacent to access road before station; 83° 02' W, 9° 40' N, 150–200 m; lowland to lower montane rain forest zone, disturbed primary and oldgrowth secondary forest, on bark (lower trunk), semi-exposed; Mar 2004, *Aptroot 60188* (BR, INB), *Lücking 17047a* (F). Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, beach north of station at mouth of Río Sirena; 83° 36' W, 8° 30' N, sea level; lowland coastal rain forest zone, disturbed coastal forest and exposed trees along beach, on bark (lower trunk), semi-exposed; Apr 2003, *Lücking 16233g* (CR, F, INB, USJ, hb. Kalb). Corcovado National Park, Los Patos Section, Los Patos Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, access trail to station and first, hilly part (5 km) of trail to Sirena; 83° 29' W, 8° 34' N, 100–300 m; lowland rain forest zone, closed primary forest, on bark (branch, fallen), exposed; Apr 2003, *Lücking 16310a* (F). Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), partially shaded; Feb 1997, *Lücking 97-131* (F, USJ).

Ocellularia subpyrenuloides* Lücking, *spec. nov. (Fig. 26C–D)
MycoBank #800096

Differing from *Ocellularia pyrenuloides* in the weakly carbonized excipulum, larger ascospores, and absence of lichen substances.

Holotype:—COSTA RICA. Puntarenas: Las Cruces Botanical Gardens, 17 km NW of San Vito; Jan 1979, *Filson 16332* (MEL).

Thallus yellow-grey, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.3–0.5 mm diam.; disc partially covered by narrow, 0.1–0.2 mm wide pore, filled by black columella; margin white-yellow, laterally covered by thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, dark brown to apically slightly carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–7-septate, 25–30 × 8–10 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This new species closely resembles *Ocellularia pyrenuloides* but the latter is readily distinguished by the presence of stictic acid, smaller ascospores, and a distinctly carbonized excipulum. The combination of brown excipulum with carbonized columella is rare in *Ocellularia* and *O. subpyrenuloides* is only the second species known with this morphotype lacking secondary substances, after *O. laeviusculoides* (see above). The latter differs mainly in thallus and apothecial morphology: the thallus is olive-grey and the columella tip is white-pruinose and surrounded by a brown proper margin.

Ocellularia supergracilis* Kalb & Lücking, *spec. nov. (Fig. 26E)
MycoBank #800097

Differing from *Ocellularia cavata* in the pink medulla and larger ascospores.

Holotype:—COSTA RICA. San José: Cordillera de Talamanca, Interamerican Highway near El Empalme, S side of the highway to San Pablo; 9° 13' N, 83° 37' W, 2200 m; lower mountain rainforest; Dec 1978, *Kalb & Plöbst 38942* (hb. Kalb).

Thallus light yellow-grey to grey-olive, uneven, with dense, paraplectenchymatous cortex; medulla pink; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia sessile, rounded, 0.7–1 mm

diam.; disc covered by 0.2–0.3 mm wide pore, filled by brown-black columella; margin entire, black beneath but covered by thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 300–350 µm high, clear; paraphyses unbranched. Ascospores 4–8/ascus, 15–25-septate, 80–130 × 7–12 µm, cylindrical to narrowly fusiform, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: cinchonarum unknowns, medulla with pink (K+ yellow then aeruginous) pigment.

Remarks:—This new species belongs in the core group of *Ocellularia* centered around *O. cavata* (see above). It is thus far the only species in the genus that combines a pink medulla with the cinchonarum unknown chemistry. All other species with that chemistry have a yellow to orange medulla and the ascospores are distinctly smaller, except for *O. rhabdospora* (see above). The latter differs from *O. supergracilis* in the unpigmented medulla and the larger apothecia. Among the few species with pink medulla in the genus, *O. rhodostroma* (see above) comes closest, but that species has a hypoprotocetraric acid chemistry and substantially larger ascospores.

Ocellularia tacarcunae* Lücking, *spec. nov. (Fig. 26F)
MycoBank #800098

Differing from *Ocellularia pluripora* in the larger ascospores.

Holotype:—PANAMA. Darien: West ridge of Cerro Tacarcuna massif; 1860 m; Jan 1975, *Mori & Gentry 4438* (US).

Thallus olive-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.6–0.9 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore; margin entire but usually with short, radiate ridges, yellow-white, laterally covered by thalline layer. Columella present but often indistinct, simple, apically carbonized. Excipulum prosoplectenchymatous, dark brown; periphysoids absent. Hymenium 180–250 µm high, clear; paraphyses unbranched. Ascospores 4/ascus, 11–15-septate, 50–70 × 10–13 µm, oblong, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This new species shares the thallus and apothecial morphology and chemistry with many other species of the genus, but is the only species with psoromic acid with medium-sized ascospores known so far. All other species with this chemistry and transversely septate ascospores have ascospores either shorter than 50 µm (usually below 30 µm) or longer than 80 µm (usually above 100 µm). Apart from ascospore size, the new species is most similar to *O. pluripora* Hale and *O. pluriporoides* (see above).

***Ocellularia terebrata* (Ach.) Müll. Arg.** (Fig. 26G)

Ocellularia terebrata (Ach.) Müll. Arg., Flora 70: 398 (1887); *Thelotrema terebratum* Ach., Kgl. Vetensk.-Akad. Nya Handl. 33: 88 (1812). Holotype. "America", s.col. (H-ACH 744!; isotypes: S!, UPS!).
Thelotrema comparabile Kremp., Flora 59: 220 (1876); *Ocellularia comparabilis* (Kremp.) Müll. Arg., Jahrb. Kgl. Botan. Garten Berlin 2: 318 (1883). Holotype. Brazil, *Glaziou 5463* (M!; isotypes: BM!, G!, PC!, UPS!).
Ocellularia comparabilis var. *microcarpa* Redinger, Arkiv Bot. 28A(8): 35 (1936). Holotype. Brazil, *Malme 726* (S!).
Ocellularia comparabilis var. *plicatula* Redinger, Arkiv Bot. 28A(8): 35 (1936). Lectotype (Frisch 2006: 258). Brazil, *Malme 3768* (S!).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.5–1 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, filled by brown-black, white-pruinose columella; margin

entire, brown, laterally covered by thalline layer. Columella present, irregular, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 90–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–9-septate, 20–32 × 6–11 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—The name *Ocellularia terebrata* has been used for a complex of species with prosoplectenchymatous cortex, small to medium-sized, erumpent apothecia with variable columella and carbonization, small, transversely septate ascospores, and psoromic acid. As a result, many synonyms have been reported for this taxon, besides those listed above including: *Pyrenula trypanea* Ach. (Frisch 2006), *Thelotrema calvescens* Fée, *Ocellularia sexlocularis* Zahlbr., and *O. pluripora* Hale (Mangold *et al.* 2009). As in the related species *O. papillata* and *O. perforata*, molecular data suggest that excessive variation is accepted at the species level in this complex (Rivas Plata *et al.* 2012b). Therefore, we separate the taxa based on presence or absence of a columella, presence or absence of distinct carbonization, and unusual combinations of a carbonized columella with pale excipulum. In *O. terebrata* s.str., both excipulum and columella are distinctly carbonized and the columella is often irregular. A carbonized columella is also found in *O. pluripora* (syn.: *Pyrenula trypanea*), but here the excipulum is orange brown. *Ocellularia calvescens* (syn.: *O. sexlocularis*), on the other hand, has a carbonized excipulum but lacks a columella.

Specimens examined:—COSTA RICA. Guanacaste: Monte Alto Forest Reserve, Monte Alto Biological Station (Tempisque Conservation Area), Nicoya Pensinsula, 150 km W of San José, 10 km SSE of Nicoya, near Hojancha, main trails and access road through reserve near station (Sendero Jardín de Orquideas, Sendero Ceiba, Sendero Shannon-Ward); 85° 24' W, 10° 02' N, 450–550 m; lowland to lower montane moist forest zone, disturbed primary and oldgrowth secondary forest, on bark (lower trunk), exposed; Mar 2004, *Sipman 51993* (B, INB). Puntarenas: Carara National Park, Quebrada Bonita Section (Pacífico Central Conservation Area), 60 km WSW of San Jose on road from Orotina to Quepos (34), trail from visitor's center to Quebrada Bonita; 84° 35' W, 9° 47' N, 100 m; lowland moist forest zone, partly disturbed dense primary forest with understory dominated by *Erythrochiton gymnanthus*, on bark (lower trunk), partially shaded; Jul 2002, *Sipman 48391a, b* (B, INB). Las Cruces Biological Station, San Vito de Coto Brus; 82° 58' W, 8° 47' N, 1200 m; trail to Río Java, on branches of fallen *Ficus pertusa* on fallen trunk; Oct 2004, *Sipman 53236* (B, INB), *53242* (B, INB), *53243* (B, INB); ibid., on ridge beyond Río Java, on trunks and undergrowth of disturbed primary forest; Oct 2004, *Sipman 53258* (B, INB); ibid., Wilson Botanical Garden; Oct 2004, *Sipman 53330* (B, INB). Las Tablas Protection Zone, Cedro Ridge, Las Alturas Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km NE of San Vito near Alturas, surroundings of station and trail into forest; 82° 50' W, 8° 57' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower trunk), partially shaded; Jun 2002, *Sipman 47815a* (B, INB), *47815b* (B, INB). Monteverde, Cordillera de Tilaran, near the cheese factory; 84° 49' W, 10° 18' N, 1450 m; premontane rain forest zone, forest relicts among pasturefields, on trunks; Jan 1979, *Sipman 12101* (U), *12120* (U).

Ocellularia terrabensis* Kalb & Lücking, *spec. nov. (Fig. 26H)
MycoBank #800099

Differing from *Ocellularia kalbii* in the smaller, hyaline ascospores and verrucose apothecial margin.

Holotype:—COSTA RICA. Puntarenas: Río Brujo Restaurant, 10 km to the Río Grande de Terraba, Interamerican Highway; 10°01’ N 85°26’ W, 350 m; Jan 1979, *Kalb & Plöbst 38949* (hb. Kalb).

Thallus light grey-olive, verrucose, with dense, paraplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent to prominent, angular-rounded, 0.7–1.2 mm diam.; disc covered by narrow, 0.1 mm wide pore, invisible; margin entire, yellow-white, laterally covered by verrucose thalline layer. Columella present, simple, carbonized. Excipulum

prosoplectenchymatous, apically dark brown; periphysoids absent. Hymenium 200–300 µm high, clear; paraphyses unbranched. Ascospores 1–2/ascus, richly muriform, 70–100 × 20–30 µm, oblong, with slightly thickened septa and rectangular lumina, becoming brown, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—Only three species within *Ocellularia* combine columellate apothecia with muriform ascospores and lack of secondary substances: *O. guptei* (Nagarkar, Sethy & Patw.) D. D. Awasthi, *O. kalbii* Mangold, and *O. sanfordiana* Zahlbr. All have persistently colorless, larger ascospores over 100 µm in length, and none has a verrucose apothecial margin.

***Ocellularia umbilicata* Müll. Arg.** (Fig. 27A)

Ocellularia umbilicata Müll. Arg., Bull. Soc. Bot. Belgique 32: 147 (1893). Holotype. Costa Rica, *Pittier 6104* (G!; isotype: US!).

Thallus yellow-brown-grey, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.3–0.5 mm diam.; disc covered by narrow, 0.1 mm wide pore, invisible; margin entire, brown, laterally covered by thalline layer. Columella absent. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 100–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 7–9-septate, 25–35 × 8–12 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—*Ocellularia umbilicata* is closely related to *O. calvescens* (see above) but has larger ascospores. It is one of the few species originally described from Costa Rica (Müller 1893). It has been found in lowland and montane rain forest.

Specimens examined:—COSTA RICA. Cartago: Tapantí National Park, Tapantí Section, Tapantí Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 35 km SE of San José and 18 km SE of Cartago, trail above road (Sendero Árboles Caidos); 83° 47' W, 9° 45' N, 1400–1600 m; montane rain forest zone, closed primary forest and roadside, on bark (branch), partially shaded; Apr 2003, *Lücking 16572* (F). Limón: Braulio Carrillo National Park, Quebrada Gonzales Section (Cordillera Volcánica Central Conservation Area), Volcánica Central Ridge, 30 km NNW of San José, trail above station (Sendero El Ceibo); 83° 56' W, 10° 10' N, 500 m; lower montane rain forest zone, primary forest, on bark (lower trunk), partially shaded; Mar 2003, *Buck 44015* (CR, NY). Puntarenas: Fila Cruces Ridge, surroundings of Las Cruces Tropical Botanical Garden, 4 km SSE of San Vito; 8° 43' N, 82° 58' W, 1550 m; in a premontane rainforest at a waterfall; Jan 1979, *Kalb & Plöbst 32017* (hb. Kalb). La Amistad International Park, Altamira Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 20 km N of San Vito near Finca Colorado, trail to Casa Coca; 82° 59' W, 9° 02' N, 1800 m; montane rain forest zone, abandoned pasture with forest remnants, on bark (lower stem), partially shaded; July 2002, *Sipman 48063g* (B, INB). Las Tablas Protection Zone, Cedro Ridge, Las Alturas Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km NE of San Vito near Alturas, surroundings of station and trail into forest; 82° 50' W, 8° 57' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower trunk), partially shaded; Jun 2002, *Sipman 47816c* (B, INB), *47816d* (B, INBio). Manuel Antonio National Park, near Quepos; 84° 09' W, 9° 23' N, sea level; scattered trees around hotel at end station of bus line; Nov 1988, *Sipman 42270b* (B, CR).

***Ocellularia urceolaris* (Ach.) Spreng.** (Fig. 27B)

Ocellularia urceolaris (Ach.) Spreng., Syst. Veget. 4(1): 242 (1827); *Thelotrema urceolare* Ach., Kgl. Vetensk.-Akad. Nya Handl. 33: 90 (1812); *Myriotrema urceolare* (Ach.) Hale, Mycotaxon 11: 135 (1980). Lectotype (Hale 1978: 55). "America", s.col. (H-ACH 746!; isolectotypes: C!, UPS!).

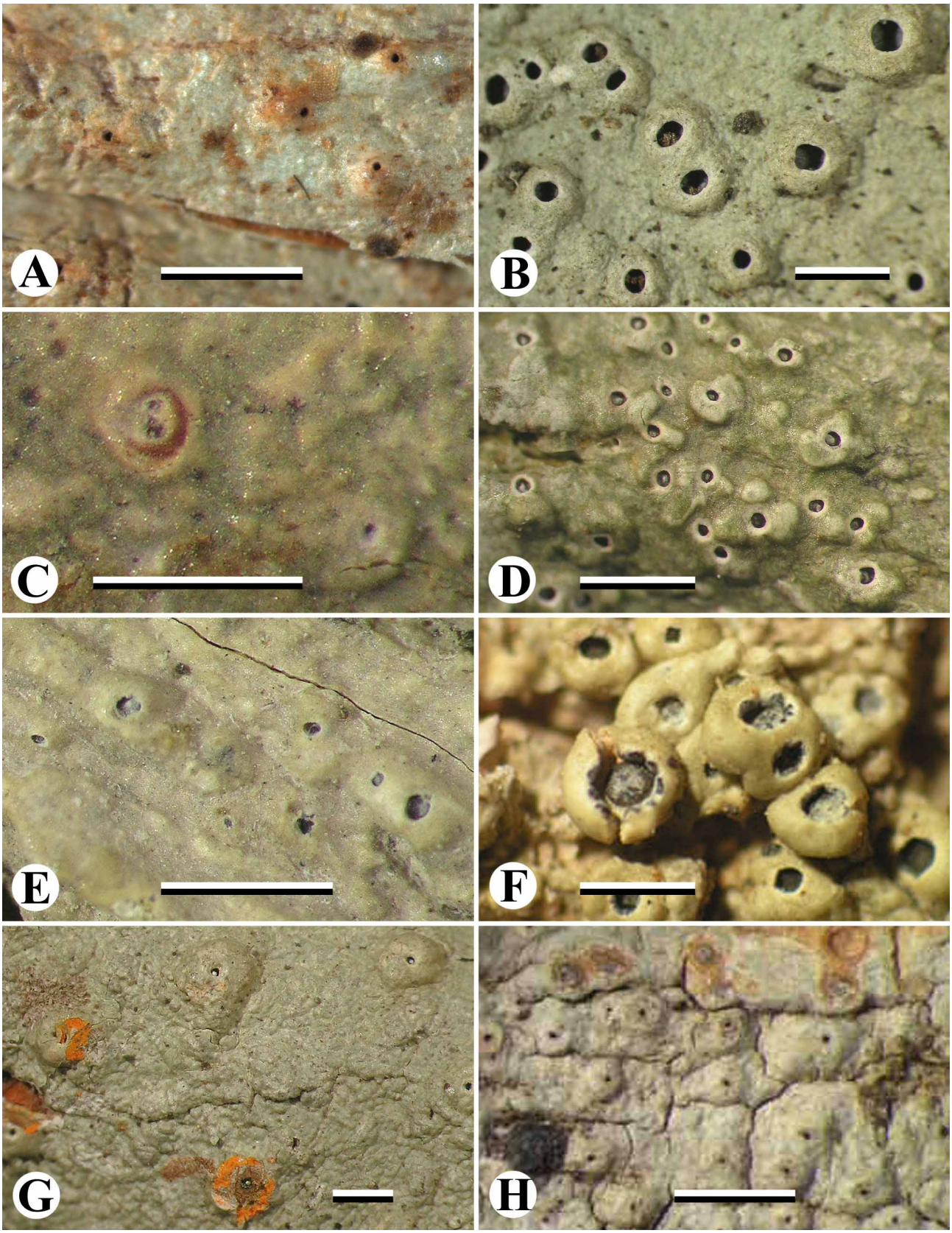

FIGURE 27. A. *Ocellularia umbilicata*. B. *Ocellularia urceolaris*. C. *Ocellularia vezdana*. D–E. *Ocellularia violacea*. F. *Ocellularia viridis*. G. *Ocellularia xanthostroma*. H. *Ocellularia zamorana*. Scale = 1 mm.

Thallus light grey-yellow-brown, smooth to uneven, with loose cortex; photobiont layer and medulla with columnar clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.7–1.1 mm diam.; disc partially covered by 0.2–0.5 mm wide pore, brown-black, white-pruinose; margin entire, brown, laterally covered by thick thalline layer. Columella absent. Excipulum prosoplectenchymatous, apically brown; periphysoids absent. Hymenium 100–130 µm high, clear; paraphyses unbranched, thick. Ascospores 8/ascus, submuriform with 3–7 transverse septa and 0–2 longitudinal septa per segment, 20–30 × 10–12 µm, ellipsoid, with thick septa and rounded lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This species is very similar to *Ocellularia bahiana* but differs in the absence of secondary substances. The lectotype material is very diminutive and appears to have a smooth thallus lacking columnar crystal clusters and the correct application of this name is uncertain.

Specimens examined:—COSTA RICA. Limón: Hitoy Cerere Biological Reserve, Hitoy Cerere Biological Station (La Amistad Caribe Conservation Area), Talamanca Ridge, 125 km ESE of San José, 40 km S of Limón, near Pandora, trails through forest above station (Sendero Espavel and Sendero Tepesquintle); 83° 02' W, 9° 40' N, 150–300 m; lowland to lower montane rain forest zone, partly disturbed primary forest, on bark (lower trunk), fully shaded; Mar 2004, *Lücking 17034* (CR, F, USJ). Puntarenas: Fila Cruces Ridge, surroundings of Las Cruces Tropical Botanical Garden, 4 km SSE of San Vito; 8° 43' N, 82° 58' W, 1550 m; in a premontane rainforest at a waterfall; Jan 1979, *Kalb & Plöbst 31642* (hb. Kalb). La Amistad International Park, Altamira Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 20 km N of San Vito near Finca Colorado, interpretative trail (Sendero Gigantes) behind station; 83° 00' W, 9° 02' N, 1500–1600 m; montane rain forest zone, disturbed primary forest and secondary vegetation dominated by *Cecropia*, on bark (lower trunk), partially shaded; Jun 2002, *Lücking 15219* (DUKE, F, INB, USJ). Las Tablas Protection Zone, Cedro Ridge, Las Alturas Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km NE of San Vito near Alturas, surroundings of station and trail into forest; 82° 50' W, 8° 57' N, 1600 m; montane rain forest zone, pasture with group of trees bordering forest, on bark (lower trunk), semi-exposed; Jun 2002, *Sipman 47818e* (B, INB); ibid., disturbed primary forest, on bark (lower stem) of Clusiaceae, partially shaded; Jun 2002, *Will-Wolf 10000b* (F, INB, WIS); ibid., on bark (lower trunk), partially shaded; Jun 2002, *Sipman 47810c* (B, INB); ibid., semi-exposed; Jun 2002, *Sipman 47820d* (B, INB). Las Tablas Protection Zone, La Neblina Section (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km ENE of San Vito near Las Mellizas, access road to fincas; 82° 45' W, 8° 55' N, 1600 m; montane rain forest zone, disturbed primary forest and pasture, on bark (trunk base), partially shaded; Jun 2002, *Nelsen 2032a* (F, INB). Wilson Botanical Garden, Las Cruces Biological Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 190 km SE of San José, trail beyond botanical garden; 82° 58' W, 8° 47' N, 1200 m; montane rain forest zone, primary forest, on bark (lower trunk), partially shaded; Sep 2007, *Lücking 21053* (F), *21067* (F). San José: San Gerardo de Dota, Finca Chacón, near entrance of Sendero La Quebrada; 83° 48' W, 9° 33' N, 2800 m; mixed, light, primary *Quercus* forest on steep slope, on thick trunk; Nov 1999, *Sipman 44328* (B 60 0107599).

***Ocellularia vezdana* Frisch** (Fig. 27C)

Ocellularia vezdana Frisch, Biblioth. Lichenol. 92: 263 (2006); *Ocellularia subterebrata* Vězda, Sched. Lich. Sel. Exs., Fasc. 30: 7, no. 748 (1969) [nom. illeg., non *O. subterebrata* (Nyl.) Zahlbr.]. Holotype. Ghana, *Jeník s.n.* (PRA-V!; isotypes: H!, M!).

Thallus grey-olive, verrucose, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.3–0.5 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, sometimes filled by brown, white-pruinose columella; margin entire, brown, laterally covered by thalline layer. Columella sometimes present, simple, pale brown. Excipulum prosoplectenchymatous, pale brown; periphysoids absent. Hymenium 80–100 µm high, clear;

paraphyses unbranched. Ascospores 8/ascus, 3–5-septate, 15–25 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: protocetraric and virensic acids.

Remarks:—This species belongs in the difficult *Ocellularia perforata* complex and is separated from *O. perforata* s.str. (see above) by the less carbonized apothecia, often absent columella, and smaller ascospores (Frisch 2006). We have used this name for a single collection that completely lacks columellae and has a brown excipulum and 5–7-septate ascospores being 20–25 µm long. It does not fit the type perfectly but there is no other name available for this material.

Specimens examined:—COSTA RICA. Puntarenas: Wilson Botanical Garden, Las Cruces Biological Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 190 km SE of San José, trail beyond botanical garden; 82° 58' W, 8° 47' N, 1200 m; montane rain forest zone, primary forest, on bark (lower trunk), fully shaded; Sep 2007, *OTS course A6AL31* (F).

***Ocellularia violacea* Räsänen** (Fig. 27D–E)

Ocellularia violacea Räsänen, Suom. Elain-ja Kasvit. Seuran Van. Tiedon. Pöytäkirjat (Arch. Soc. Zool. Bot. Fenn. Vanamo) 3: 184 (1949). Holotype. Australia, *Wilson s.n.* (H-Räsänen!).

Thallus grey-olive, verrucose, with dense, paraplectenchymatous cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.3–0.8 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, filled by brown-black, white-pruinose columella; margin entire, yellow-white, laterally covered by thalline layer. Columella present, simple, carbonized. Excipulum prosoplectenchymatous, brown; periphysoids absent. Hymenium 80–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–7-septate, 15–25 × 7–8 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: protocetraric and virensic acids.

Remarks:—This taxon was considered a synonym of *Ocellularia perforata* (Mangold *et al.* 2009) but is here kept separate due to the unusual combination of pale excipulum and distinctly carbonized columella. Like *O. papillata*, *O. perforata* is considered a variable species with regard to carbonization (Mangold *et al.* 2009; Papong *et al.* 2010), but this seems to reflect an ad-hoc concept rather than thorough analysis of the available material. *Ocellularia violacea* was commonly found at mid elevations in very humid rain forests.

Specimens examined:—COSTA RICA. Alajuela: San Ramón Forest Reserve, near house at Río Lorencito, c. 5 km NE of Cerro Jabonal; 84° 37' W, 10° 13' N, 1000 m; humid, mossy forest with many ferns on mountain ridge, on thin trunk in undergrowth; Nov 1988, *Sipman et al. 41961* (B, CR), *41965* (B, CR), *41975* (B, CR), *41991* (B, CR). Volcán Tenorio National Park, Pilón Biological Station (Arenal-Tempisque Conservation Area), Tilarán Ridge, 140 km NW of San José, 25 km NNW of Tilarán, near Bijagua, main trail through forest to crater; 84° 59' W, 10° 43' N, 700–900 m; lower montane cloud forest zone, partly disturbed primary forest, on bark (twig), partially shaded; Mar 2004, *Lücking 17261b* (CR, F). Puntarenas: La Amistad International Park, Altamira Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 20 km N of San Vito near Finca Colorado, interpretative trail (Sendero Gigantes) behind station; 83° 00' W, 9° 02' N, 1500–1600 m; montane rain forest zone, disturbed primary forest and secondary vegetation dominated by *Cecropia*, on bark (lower stem), partially shaded; Jun 2002, *Lücking 15215* (F, INB, USJ). Wilson Botanical Garden, Las Cruces Biological Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 190 km SE of San José, trail beyond botanical garden; 82° 58' W, 8° 47' N, 1200 m; montane rain forest zone, primary forest, on bark (lower trunk), fully shaded; Sep 2007, *Lücking 21069* (F), *OTS course A1JT23* (F). Near Las Cruces Garden, c. 4 km SSE of San Vito; 82° 57' W, 8° 43' N, 1300 m; premontane rain forest zone, on scattered, thick, tall trunks in pasture on slope; Dec 1978, *Sipman 11893* (B). Las Tablas Protection Zone, La Neblina Section (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km ENE of San Vito near Las Mellizas, access road to fincas; 82° 45' W, 8° 55' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower trunk), partially shaded; Jun 2002, *Sipman 47887a* (B, INB).

***Ocellularia viridis* Hale** (Fig. 27F)

Ocellularia viridis Hale, Smithson. Contr. Bot. 38: 34 (1978). Holotype. Panama, *Hale 38538* (US!).

Thallus light grey-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia sessile, rounded, 0.6–1 mm diam.; disc partially covered by 0.1–0.3 mm wide pore, flesh-colored, partly filled by white pseudocolumella; margin entire, yellow-white, laterally covered by thalline layer. Pseudocolumella present, irregular, white. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 60–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–5-septate, 10–15 × 5–7 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: viridis unknown (exposed medulla P–; section K–).

Remarks:—*Ocellularia viridis* is a highly unusual species within the genus, characterized by the sessile apothecia, the carbonized excipulum in combination with an uncarbonized pseudocolumella, and the viridis unknown substance. Morphologically most similar is *O. mauritiana* (see above), which has an uncarbonized excipulum and protocetraric acid.

Specimens examined:—The species is not yet known from Costa Rica, but has been reported from Panama (Hale 1978).

***Ocellularia xanthostroma* (Nyl.) Zahlbr.** (Fig. 27G)

Ocellularia xanthostroma (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 603 (1923); *Ascidium rhodostroma* var. *xanthostroma* Nyl., Ann. Sci. Nat. Bot., Ser. 4, 19: 335 (1863). Lectotype (Hale 1978: 34). Cuba, *Wright 33* (H-NYL 22412!).

Thallus light grey-green, verrucose, with dense, paraplectenchymatous cortex; medulla orange; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, angular-rounded, 1–1.5 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, invisible; margin grey, laterally covered by partially eroding thalline layer. Columella absent. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 250–350 µm high, clear; paraphyses unbranched. Ascospores 2–4/ascus, 15–39-septate, 80–200 × 10–20 µm, oblong-fusiform with shortly caudate ends and gelatinous caps, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: medulla with orange pigment (K–); otherwise no substances detected by TLC.

Remarks:—This taxon belongs in a group of species with pigmented medulla, robust, carbonized apothecia, and large, multiseptate ascospores. *Ocellularia mordenii* (see above) differs chiefly in the cinnabar-red (K+ dark red) instead of orange (K–) pigment, whereas *O. rhodostroma* (see above) has a pink pigment and in addition hypoprotocetraric acid.

Specimens examined:—COSTA RICA. Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, second part of trail from Los Patos to Sirena station; 83° 33' W, 8° 32' N, sea level; lowland rain forest zone, oldgrowth secondary forest and closed secondary vegetation, on bark (lower stem), semi-exposed; Apr 2003, *Sipman 51088g* (B, CR), *51089b* (B, INB), *51096* (B, INB), *51103e* (B, CR). Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), partially shaded; Feb 1997, *Lücking 97-249* (F).

Ocellularia zamorana* Sipman, Lücking & Chaves, *spec. nov. (Fig. 27H)
MycoBank #800100

Differing from *Ocellularia albula* in the apothecia with wider pore and brown excipulum and 3-septate ascospores.

Holotype:—COSTA RICA. San José: San Gerardo de Dota, Finca Chacón, near entrance of Sendero La Quebrada; 83° 48' W, 9° 33' N, 2800 m; mixed, light, primary *Quercus* forest on steep slope, on thin trunk; Nov 1999, *Sipman 44326* (INB-0003907562; isotype: B).

Thallus pale green-grey, smooth to uneven, with dense, paraplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.4–0.5 mm diam.; disc covered by 0.1 mm wide pore, brown, thinly white-pruinose; margin entire, white-yellow, laterally covered by thalline layer. Columella absent. Excipulum prosoplectenchymatous, colorless; periphysoids absent. Hymenium 100–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5-septate, 15–20 × 5–6 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ brown-violet (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—In spite of a large number of species in *Myriotrema* and *Ocellularia* with small, transversely septate ascospores and psoromic acid, we have not found a name for this rather characteristic collection. The recently described *Myriotrema temperatum* Mangold from Australia is most similar but differs in its myriotremoid apothecia and 3-septate ascospores. *Fibrillithecis pachystoma* (see above) has much larger apothecia with apical fibrils and also 3-septate ascospores. *Myriotrema fragile* (Hale) Hale has larger, erumpent apothecia, 3-septate ascospores, and a fragile thallus. *Ocellularia albula* (Nyl.) Zahlbr. is the most similar species in *Ocellularia*, but differs by its apothecia with wider pore and dark brown excipulum and also by its 3-septate ascospores. Other similar species in *Ocellularia*, such as *O. minutula* (see above), feature a columella. This new species is dedicated to Dr. Rodrigo Bolaños Zamora, researcher at the Inter-American Development Bank in Costa Rica and benefactor of INBio.

Pycnotrema Rivas Plata & Lücking

Pycnotrema Rivas Plata & Lücking in Rivas Plata *et al.*, Fungal Diversity 52: 118 (2011). Type. *Pycnotrema pycnoporellum* (Nyl.) Rivas Plata & Lücking.

Thallus light grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed, rounded; disc covered by narrow pore; margin entire, fused, laterally covered by thalline layer. Columella absent. Excipulum prosoplectenchymatous, brown; periphysoids absent. Paraphyses unbranched. Ascospores submuriform, small, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances.

Remarks:—This genus was established by Rivas Plata *et al.* (2011a) to accommodate a single species, *P. pycnoporellum*, that morphologically resembles a typical *Myriotrema* but clusters with the *Fissurina* clade, quite distant from *Myriotrema* in the *Ocellularia* clade (Rivas Plata & Lumbsch 2011a). Other than the molecular data, there are no characters distinguishing *Pycnotrema* from species of *Myriotrema* lacking secondary substances.

Pycnotrema pycnoporellum (Nyl.) Rivas Plata & Lücking (Fig. 28A)

Pycnotrema pycnoporellum (Nyl.) Rivas Plata & Lücking in Rivas Plata *et al.*, Fungal Diversity 52: 118 (2011); *Myriotrema pycnoporellum* (Nyl.) Hale, Mycotaxon 11: 135 (1980); *Thelotrema pycnoporellum* Nyl., Flora 59: 562

(1876); *Thelotrema* '*pycnocarpellum*' Nyl. in Zahlbruckner, Cat. Lich. Univ. 2: 628 (1923) [orthographic error]. Lectotype (Hale 1978: 47). Cuba, *Wright 69* (H-NYL 22682!; isolectotypes: FH!, G!, UPS!).

Thallus light grey-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia immersed, rounded, 0.1–0.3 mm diam., often aggregate in lines; disc covered by narrow, 0.05–0.1 mm wide pore, invisible; margin entire, brown-black. Columella absent. Excipulum prosoplectenchymatous, brown; periphysoids absent. Hymenium 60–70 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–1 longitudinal septa per segment, 20–24 × 8–10 µm, ellipsoid, with thick septa and rounded lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This species is recognized by its very small apothecia with brown-black rim around the narrow pore, in combination with small, submuriform ascospores and lack of secondary substances. *Myriotrema subconforme* agrees in ascospores and chemistry but has larger apothecia with free excipulum.

Specimens examined:—COSTA RICA. Cartago: On road Limón-Turrialba, about halfway between Siquirres and Chitaría; 10° 03' N, 83° 30' W, 700 m; on trunks in grazed parkland with groves; Jan 1979, *Sipman 12351* (B). Tapantí National Park, Tapantí Section, Tapantí Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 35 km SE of San José and 18 km SE of Cartago, road above second trail to river (Sendero La Pava) below Mirador; 83° 47' W, 9° 44' N, 1700 m; montane cloud forest zone, primary forest margin along roadside, on bark (lower trunk), semi-exposed; Apr 2003, *Buck 44151* (CR, NY). Heredia: La Selva Protection Zone, La Selva Biological Station (Cordillera Volcánica Central Conservation Area), Volcánica Central Ridge, 55 km N of San Jose, Arboleda; 84° 03' W, 10° 26' N, 50 m; lowland rain forest zone, disturbed primary and secondary forest, on bark (lower trunk), partially shaded; Oct 2002, *Lücking 16045* (F). Limón: Hitoy Cerere Biological Reserve, Hitoy Cerere Biological Station (La Amistad Caribe Conservation Area), Talamanca Ridge, 125 km ESE of San José, 40 km S of Limón, near Pandora, trail along Río Estrella to waterfall; 83° 02' W, 9° 40' N, 150 m; lowland to lower montane rain forest zone, secondary vegetation and disturbed primary forest along river, on bark (root), partially shaded; Mar 2004, *Lücking 17008a* (F, INB).

Redingeria Frisch

Redingeria Frisch in Frisch & Kalb, Biblioth. Lichenol. 93: 402 (2006). Type. *Redingeria leiostoma* (Nyl.) Frisch.

Thallus light grey-olive to yellow-grey, with loose cortex or rarely ecorticate or with dense cortex. Apothecia immersed to prominent, angular-rounded to elongate-lirellate; disc partially covered; margin entire to fissured or rarely lobulate, fused. Columella usually present, broad-stump-shaped to irregular or reticulate, mostly carbonized. Excipulum prosoplectenchymatous, mostly carbonized; periphysoids absent. Paraphyses unbranched. Ascospores septate to submuriform, ellipsoid, with thick septa and walls and lens-shaped to irregular lumina, dark brown, I– when mature but I+ violet-blue (amyloid) when young and lacking pigment. Secondary chemistry: no substances or hypoprotocetraric acid and/or lichexanthone.

Remarks:—*Redingeria* is very similar to *Melanotrema* morphologically and mainly distinguished by the thick-walled ascospores with a slightly different ontogeny as well as hypoprotocetraric acid as frequent compound (Frisch & Kalb 2006). While these differences appear minor, the two genera are well separated genetically (Rivas Plata *et al.* 2012b).

Key to the species of *Redingeria* found or expected in Costa Rica (4)

1. Ascospores 1–2-septate; no substances ..... ***R. vulcani***
- Ascospores 3-septate to submuriform; lichexanthone 2

2. Ascospores submuriform; excipulum carbonized; lichexanthone only ..... ***R. microspora***
- Ascospores 3-septate; excipulum brown; hypoprotocetraric acid in addition to lichexanthone 3

3. Apothecia annulate, round to elongate with narrow pore or slit; columella mostly simple ..... ***R. leiostoma***
- Apothecia not annulate, angular-rounded to elongate with more or less exposed disc and irregular to reticulate columella ..... ***R. glyphica***

***Redingeria glyphica* (Nyl.) Frisch** (Fig. 28B)

Redingeria glyphica (Nyl.) Frisch, Biblioth. Lichenol. 92: 411 (2006); *Thelotrema glyphicum* Nyl., Acta Soc. Sci. Fenn. 7: 453 (1863); *Ocellularia glyphica* (Nyl.) Hale, Mycotaxon 11: 136 (1980). Lectotype (Hale 1978: 36). Colombia, *Lindig 826* (FH!; isolectotypes: BM!, H-NYL 22681!, M!).

Thallus grey-olive, verrucose, with loose cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular to lirellate, 0.5–4 × 0.5–0.8 mm large; disc partially covered by 0.3–0.5 mm wide pore, partly filled by brown-black, white-pruinose columella; margin fissured, pale brown, laterally covered by thalline layer. Columella present, broad-stump-shaped to reticulate, carbonized. Excipulum prosoplectenchymatous, brown; periphysoids absent. Hymenium 100–140 µm high, clear; paraphyses unbranched, thick. Ascospores 8/ascus, 3-septate, 17–22 × 8–10 µm, ellipsoid, with thick septa and lens-shaped lumina, brown, mature I– but young I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids, lichexanthone.

Remarks:—This species resembles a *Stegobolus* due to its exposed disc and the broad columella becoming reticulate. There are two species currently classified in *Stegobolus* that share the following characters with *R. glyphica*: *S. metaphoricus* with lichexanthone and brown, submuriform ascospores and *S. actinotus* with hypoprotocetraric acid. The generic placement of these species must be considered provisional until sequenced. However, they differ from *R. glyphica* in the more greenish, smooth thallus.

Specimens examined:—COSTA RICA. Chirripó National Park, trail from Crestones to San Gerardo, near entrance gate; 9° 29' N, 83° 29' W, 2200 m; disturbed primary mossy mountain forest, on trunk along trail; Mar 2000, *Sipman & Umaña 46576* (B, INB).

***Redingeria leiostoma* (Tuck.) Frisch** (Fig. 28C)

Redingeria leiostoma (Tuck.) Frisch, Biblioth. Lichenol. 92: 416 (2006); *Thelotrema leiostomum* Tuck., Proc. Amer. Acad. Arts Sci. 5: 407 (1862); *Ocellularia leiostoma* (Tuck.) Harris, Some Florida Lichens: 93 (1990). Holotype. Cuba, *Wright s.n.* (FH!; Wright, Lich. Cubae 149; isotype: H-NYL 22857!).

Thallus grey-olive, smooth to uneven, with loose cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, round to lirellate or several apothecia forming a line, 0.5–3.5 × 0.5–1.1 mm large; disc covered by narrow, 0.1–0.2 mm wide pore, filled by brown-black, white-pruinose columella; margin annulate, pale brown, laterally covered by thalline layer. Columella present, simple to irregular, carbonized. Excipulum prosoplectenchymatous, brown; periphysoids absent. Hymenium 100–120 µm high, clear; paraphyses unbranched, thick, apically capitate. Ascospores 8/ascus, 3-septate, 16–21 × 8–10 µm, ellipsoid, with thick septa and lens-shaped lumina, brown, mature I– but young I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids, lichexanthone.

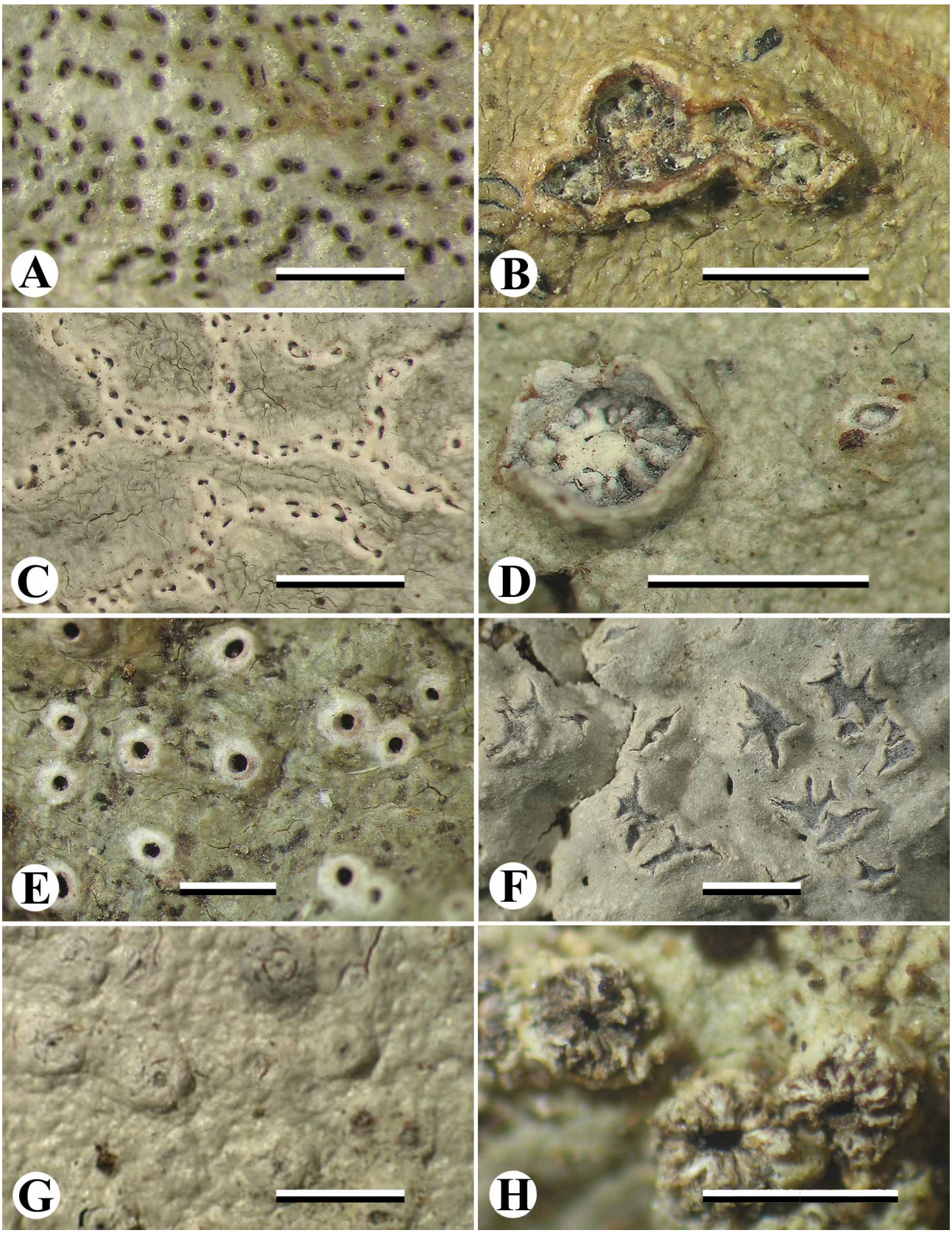

FIGURE 28. A. *Pycnotrema pycnoporellum*. B. *Redingeria glyphica*. C. *Redingeria leiostoma*. D. *Redingeria microspora*. E. *Redingeria vulcani*. F. *Reimnitzia santensis*. G. *Schizotrema cryptotrema*. H. *Schizotrema guadeloupense*. Scale = 1 mm.

Remarks:—This species is rather characteristic due to the narrow, annulate apothecia resembling a *Myriotrema* but often arranged in a line or becoming elongate-lirellate. There is no other similar species in the family.

Specimens examined:—Not yet known from Costa Rica, but reported from Panama (Hale 1978).

***Redingeria microspora* (Zahlbr.) M. E. Cáceres & Lücking** (Fig. 28D)

Redingeria microspora (Zahlbr.) M. E. Cáceres & Lücking in Cáceres et al., Lichenologist 44 (in press); *Leptotrema microsporum* Zahlbr., Sitzungsber. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Klasse 111: 392 (1902); *Thelotrema microsporoides* Zahlbr., Cat. Lich. Univ. 2: 625 (1923) [nom. nov., non *T. microsporum* Mont.]. Lectotype (Hale 1978: 53). Brazil, *von Höhnel 148* (W!).

Thallus light grey-olive, with minutely grainy surface, with loose cortex; photobiont layer and/or medulla with columnar clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.5–0.8 mm diam.; disc partially covered by 0.2–0.5 mm wide pore, filled by brown-black, white-pruinose columella; margin fissured, fused, brown-black, white-pruinose. Columella present, broad-stump-shaped to reticulate, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 70–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, ellipsoid, submuriform with 3 transverse and 0–1 longitudinal septa per segment, 10–15 × 7–11 µm, with thick septa and lens-shaped lumina, brown, mature I– but young I+ violet-blue (amyloid). Secondary chemistry: lichexanthone.

Remarks:—*Redingeria microspora* is a good example of the difficulty to tell apart species in *Melanotrema*, *Redingeria*, and *Stegobolus*. Hale (1978) compared the species with *Stegobolus metaphoricus*, as both share the chemistry (lichexanthone) and the small, submuriform, brown ascospores. Young apothecia of *S. metaphoricus* are very similar to young apothecia of *R. microspora*, but with age those of the former become lirellate whereas those of *R. microspora* remain angular-rounded. Another difference is the yellow-green thallus with smooth surface in *S. metaphoricus* versus the grey-olive thallus with grainy surface in *R. microspora*. Hale (1980) combined the species as *Ocellularia microspora* (Zahlbr.) Hale, but Frisch & Kalb (2006) eventually synonymized it with *Stegobolus metaphoricus*. *Melanotrema astrolucens* (Sipman) Frisch is another similar species that resembles a *Stegobolus* due to its dense cortex and which produces lichexanthone on the apothecia only. *Ocellularia marivelensis* (Vain.) Hale is very similar to *Redingeria microspora* in thallus and apothecial morphology and anatomy, but produces psoromic acid instead of lichexanthone. Molecular phylogenetic analysis places *R. microspora* in *Redingeria* and *O. marivelensis* in *Stegobolus* s.lat., specifically in the *Rhabdodiscus* group (see below; Rivas Plata *et al.* 2012b).

The name *Thelotrema microsporoides* is apparently based on a mishap. Zahlbruckner (1923) listed this name under *Thelotrema*, indicating '*Thelotrema microsporum* Zahlbr.' as basionym and *T. microsporum* Mont. as competing homonym. It is unclear whether Zahlbruckner actually intended to combine *Leptotrema microsporum* in *Thelotrema* and erroneously cited the basionym as *Thelotrema* instead of *Leptotrema*, or whether he thought that he had described the species as *Thelotrema* and believed that this was a later homonym of *T. microsporum* Mont.

Specimens examined:—COSTA RICA. Guanacaste: Lomas de Barbudal Biological Reserve, Lomas de Barbudal Station (Tempisque Conservation Area), Río Tempisque Bassin, 140 km WNW of San José and 20 km WSW of Bagaces, trail from station to Río Barbudal; 85° 22' W, 10° 30' N, 100 m; lowland to lower montane moist forest zone, disturbed gallery forest and forest remnants, on bark (lower trunk), partially shaded; Mar 2003, *Will-Wolf 12522* (F, INB, WIS); ibid., on bark (branch, fallen), exposed; Mar 2003, *Buck 43989* (CR, F, NY); ibid., on bark (lower trunk), exposed; Mar 2003, *Lücking 16110* (INB).

Redingeria vulcani* (Hale) Lücking, *comb. nov. (Fig. 28E)
MycoBank #800063

Phaeotrema vulcani Hale, Smithson. Contr. Bot. 38: 37 (1978); *Myriotrema vulcani* (Hale) Hale, Mycotaxon 11: 135 (1980). Holotype. Panama, *Hale 43534* (US!).

Thallus light grey-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.5–0.7 mm diam.; disc partially covered by 0.2–0.3 mm wide pore, flesh-colored, partly filled by white pseudocolumella; margin entire, becoming annulate, yellow-white, laterally covered by thalline layer. Pseudocolumella present, irregular, white. Excipulum prosoplectenchymatous, pale brown; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 1–2-septate, 10–16 × 4–6 µm, ellipsoid, with thick septa and lens-shaped lumina, brown, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This species is here combined into *Redingeria* due to its morphological similarities with the type species and the ascospores resembling those of other species of the genus. It is most similar to *R. deightonii* which differs mainly in the 3-septate, larger ascospores.

Specimens examined:—Not yet known from Costa Rica, but reported from Panama (Hale 1978).

Reimnitzia Kalb

Reimnitzia Kalb, Mycotaxon 79: 325 (2001). Type. *Reimnitzia santensis* (Tuck.) Kalb..

Thallus grey-olive with bluish tinge, smooth to uneven and with minutely grainy surface, gall-forming, producing isidia, ecorticate; isidia cylindrical, often with hair-like projections apically; photobiont layer and medulla with columnar clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded; disc exposed, brown-black, white-pruinose; margin lobulate to recurved, white-grey. Columella absent. Excipulum paraplectenchymatous, brown; periphysoids absent. Paraphyses apically branched, thick. Ascospores 8/ascus, ellipsoid, submuriform, with thick septa and rounded lumina, brown, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Reimnitzia* features chroodiscoid apothecia and hence resembles the genus *Chapsa* in general appearance. However, the lack of periphysoids and the apically branched paraphyses separate the genus from *Chapsa*. Apothecial anatomy, ascospore type, and thallus structure agree with the genus *Leptotrema*, with which *Reimnitzia* is closely related (Rivas Plata & Lumbsch 2011a, b; Rivas Plata *et al.* 2012b). However, *Leptotrema* has myriotremoid apothecia, i.e. small immersed pores with entire margin.

***Reimnitzia santensis* (Tuck.) Kalb** (Fig. 28F)

Reimnitzia santensis (Tuck.) Kalb, Mycotaxon 79: 325 (2001); *Thelotrema santense* Tuck., Proc. Amer. Acad. Arts Sci. 5: 406 (1862). Lectotype (Salisbury 1972b: 288). U.S.A., *Ravenel s.n.* (BM!).
Thelotrema heterosporum C. Knight in Bailey, Synops. Queensland Flora, Suppl. 1: 72 (1886); *Leptotrema heterosporum* (C. Knight) Zahlbr., Cat. Lich. Univ. 2: 635 (1923). Holotype. Australia, Knight s.n. (WELT, not seen).
Leptotrema mastoideum Müll. Arg., Flora 70: 400 (1887). Holotype. Paraguay, *Balansa 38* (G!).
Phaeotrema biloculare C. W. Dodge in Frisch, Biblioth. Lichenol. 92: 273 (2006); nom. inval. Original material: Mozambique, *Gommes & Sousa s.n.* (BM!, FH!).

Thallus light grey-olive with bluish tinge, smooth to uneven with minutely grainy surface, gall-forming, producing isidia, ecorticate; isidia up to 1 mm long and 0.1–0.2 mm thick; photobiont layer and/or medulla with columnar clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.5–1 mm diam.;

disc exposed, brown-black, white-pruinose; margin lobulate to recurved, white-grey. Columella absent. Excipulum paraplectenchymatous, brown; periphysoids absent. Hymenium 80–120 µm high, clear; paraphyses apically branched, thick. Ascospores 8/ascus, submuriform with 3 transverse septa and 0–1 longitudinal septa per segment, 13–23 × 9–11 µm, ellipsoid, submuriform 3 transverse and 0–1 longitudinal septa per segment, with thick septa and rounded lumina, brown, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Reimnitzia santensis* is one of the most distinctive species in the family, easily recognized by the gall-forming, fragile, ecorticate thallus producing rather large isidia. The chroodiscoid apothecia are not as commonly produced as the isidia. Although *Leptotrema* is the closest relative, *Reimnitzia santensis* is also reminescent of *Leucodecton* species, in particular *L. glaucescens*, which because of its chroodiscoid apothecia and gall-forming thallus may look like a diminutive *Reimnitzia santensis*. However, molecular data show that the two genera are not related and the superficial similarities must be interpreted as parallel evolution (Rivas Plata & Lumbsch 2011a, b). The name *Phaeotrema biloculare* C. W. Dodge was added to the synonymy by Frisch (2006) but has not been validly published.

Specimens examined:—COSTA RICA. Guanacaste: Barra Honda National Park, Barra Honda Biological Station (Tempisque Conservation Area), Barra Honda Mountains, 140 km WNW of San José, 10 km ENE of Nicoya, main trail to Terciopelo cave and Mirador; 85° 21' W, 10° 10' N, 400–500 m; lowland to lower montane moist forest zone, disturbed primary and oldgrowth secondary forest with calcareous rock outcrops, on bark (lower trunk), semi-exposed; Mar 2004, *Aptroot 60838* (BR, INB). Hacienda Granadilla, hills south of farmhouse; 500–600 m; Feb 1930; *Dodge & Thomas 6633*, *6705*, *6717*, *6735* (FH, as *Leptotrema glaucescens* var. *epileptum* (Nyl.) Zahlbr. and *Phaeotrema meiospermum* (Nyl.) Müll. Arg.). Lomas de Barbudal Biological Reserve, Lomas de Barbudal Station (Tempisque Conservation Area), Río Tempisque Bassin, 140 km WNW of San José and 20 km WSW of Bagaces, trail from station to Río Barbudal; 85° 22' W, 10° 30' N, 100 m; lowland to lower montane moist forest zone, disturbed gallery forest and forest remnants, on bark (lower stem), semi-exposed; Mar 2003, *Sipman 51047b* (B, INB). Puntarenas: Las Tablas Protection Zone, La Neblina Section (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km ENE of San Vito near Las Mellizas, access road to fincas; 82° 45' W, 8° 55' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower trunk), partially shaded; Jun 2002, *Will-Wolf 10024b* (INB, WIS). Monte Verde, Cordillera de Tilaran, ca. 20 km E of Juntas; Jan 1979, *Filson 16381a* (MEL).

Schizotrema Mangold & Lumbsch

Schizotrema Mangold & Lumbsch in Mangold *et al.*, Fl. Australia 57: 657 (2009). Type. *Schizotrema zebrinum* Mangold.

Thallus usually light grey-olive to yellowish olive, smooth to uneven, with loose to dense, irregular or prosoplectenchymatous cortex; photobiont layer and medulla often with clusters of calcium oxalate crystals. Apothecia immersed to prominent, rounded to angular-rounded; disc covered by more or less narrow pore formed by innermost excipulum layers; margin fissured to lobulate, fused or partially free, brown to black, laterally covered by thalline layer, becoming multilayered in older apothecia. Columella absent. Excipulum prosoplectenchymatous, colorless to usually dark brown or carbonized; periphysoids present. Paraphyses unbranched. Ascospores transversely septate to muriform, small to large, ellipsoid-fusiform to oblong, with thin to slightly thickened septa and rectangular lumina, colorless or light brown, I– or I+ weakly violet-blue (amyloid) in some species. Secondary chemistry: variable, including psoromic, hypoprotocetraric, stictic, and salazinic acids and cinchonarum unknown.

Remarks:—*Schizotrema* is a recently established genus accommodating species with more or less thelotremoid apothecia that feature a multilayered margin with usually carbonized excipulum (Mangold *et al.* 2009). Most similar in terms of apothecial anatomy are the genera *Melanotopelia* and *Topeliopsis*, but both

have usually sessile apothecia overgrowing bryophytes. *Melanotopelia* lacks a layered and lobulate margin, whereas *Topeliopsis* has an always pale excipulum. Genetically, these genera are well-separated (Rivas Plata *et al*. 2012c), but the placement of individual species in either genus is more questionable; for example, several species currently placed in *Thelotrema* s.lat. share features with *Schizotrema* but have either amyloid ascospores or an uncarbonized excipulum (Rivas Plata *et al*. 2010a).

Key to the species of *Schizotrema* found or expected in Costa Rica (2)

1. Stictic acid; excipulum distinctly carbonized ..... ***S. guadeloupense***
- Psoromic acid; excipulum indistinctly carbonized at apex..... ***S. cryptotrema***

***Schizotrema cryptotrema* (Nyl.) Rivas Plata & Mangold** (Fig. 28G)

Schizotrema cryptotrema (Nyl.) Rivas Plata & Mangold in Rivas Plata *et al.*, Lichenologist 42: 184 (2010); *Thelotrema cryptotrema* Nyl., Ann. Sci. Nat. Bot., Sér. 5, 7: 318 (1867). *Ocellularia cryptotrema* (Nyl.) Kalb, Lich. Neotrop., Fasc VII: no. 283 (1983). Lectotype (Hale 1978: 43): French Guiana, *Melinou s.n.* (H-NYL 22490!).

Thelotrema annulatum Müll. Arg., J. Linn. Soc. London 30: 453 (1895). Lectotype (Hale 1978: 43). Brazil, *Glaziou 5474* (G!; isolectotype: BM!).

Thelotrema secoligella Müll. Arg., Hedwigia 34: 31 (1895). Lectotype (Hale 1978: 43). French Guiana, *Leprieur 722* (G!).

Thallus white-grey, smooth to uneven, with dense cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.4–0.6 mm diam.; disc covered by narrow, 0.05–0.1 mm wide pore, invisible; margin fissured to lobulate, grey to brown-black, layered, covered by thalline layer. Columella absent. Excipulum paraplectenchymatous, apically dark brown to carbonized; periphysoids present. Hymenium 150–200 µm high, clear; paraphyses unbranched. Ascospores 1–4/ascus, richly muriform, 55–80 × 15–30 µm, ellipsoid, with slightly thickened septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids (medulla P+ yellow; section K–; surface UV–).

Remarks:—The circumscription of this taxon is somewhat unclear. The Costa Rican material shows only weak excipular carbonization, but the type of *Thelotrema cryptotrema* itself is variable in this respect, having apothecia with pale to dark brown or apically carbonized excipulum on the same thallus. Since the other features of this species, in particular psoromic acid combined with non-amyloid ascospores and thelotremoid apothecia, are rather unusual, we opted for treating the variation in excipular carbonization under one species.

Specimens examined:—COSTA RICA. Cartago: Río Macho Forest Reserve, La Esperanza del Guarco, c. 10 km S of El Empalme on road to San Isidro del General; 9° 41' N, 83° 55' W, 2500 m; primary, c. 25 m tall *Quercus* forest on mountain slope, on tree base; Nov 1999, *Sipman 44310* (B). Guanacaste: Monte Alto Forest Reserve, Cerro Romo (Tempisque Conservation Area), Nicoya Pensinsula, 150 km W of San José, 15 km SSE of Nicoya, near Hojancha, access road to and surroundings of Mirador; 85° 24' W, 10° 00' N, 750–900 m; lowland to lower montane moist forest zone, exposed trees and fence posts along pasture, on bark (lower trunk), exposed; Mar 2004, *Aptroot 60884* (BR, INB). Puntarenas: Manuel Antonio National Park, near Quepos 9° 23' N, 84° 09' W, sea level; scattered trees around hotel at end station of bus line; Nov 1988, *Sipman 42269* (B, CR).

***Schizotrema guadeloupense* (Hale) Mangold & Lumbsch** (Fig. 28H)

Schizotrema guadeloupense (Hale) Mangold & Lumbsch, Fl. Australia 57: 657 (2009); *Thelotrema guadeloupense* Hale [as '*guadeloupensis*'], Phytologia 26: 416 (1973). Holotype. Lesser Antilles (Guadeloupe), *Hale 31633* (US!).

Thallus light grey-olive-yellow, smooth to uneven, with loose cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, angular-rounded, 0.8–1 mm diam.; disc covered by narrow, 0.1–0.3 mm wide pore and inner layers of excipulum, invisible; margin fissured to lobulate, brown-black, layered, laterally covered by thalline layer. Columella absent. Excipulum paraplectenchymatous, carbonized; periphysoids present, distinct. Hymenium 120–160 µm high, clear; paraphyses unbranched. Ascospores 4–8/ascus, richly muriform, 30–80 × 15–25 µm, ellipsoid, with slightly thickened septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: stictic acid, constictic, and α-acetylhypoconstictic acids.

Remarks:—This species is rather similar to *Schizotrema cryptotrema* but differs in the stictic acid chemistry and the more prominent apothecia, as well as the higher number of ascospores per ascus.

Specimens examined:—COSTA RICA. Alajuela: Volcán Poás National Park; 10° 12' N, 84° 46' W, 2700 m; stunted dwarfforest on rim of old crater around Laguna Botos, epiphyte; Mar 1985, *Sipman 20875* (B, CR).

Stegobolus Mont.

Stegobolus Mont., Hooker's London J. Bot. 4(3): 4 (1845). Type. *Stegobolus berkeleyanus* Mont.

Thallus usually grey-olive, smooth to uneven or verrucose, usually with dense, prosoplectenchymatous cortex; photobiont layer and medulla (if developed) with clusters of calcium oxalate crystals. Apothecia prominent to sessile, angular-rounded to elongate-lirellate; disc partially covered to exposed, usually filled by columella; margin entire to fissured-lobulate, laterally covered by thalline layer. Columella present, broad-stump-shaped to lobate-reticulate or radiate, pale brown to carbonized, usually white-pruinose. Excipulum prosoplectenchymatous, brown to carbonized; periphysoids absent. Paraphyses unbranched. Ascospores transversely septate to muriform, small, ellipsoid-fusiform to oblong, with thick septa and lens-shaped lumina, colorless or brown, I+ violet-blue (amyloid) at least when young. Secondary chemistry: variable, frequently psoromic acid and satellite substances.

Remarks:—The genus *Stegobolus* was resurrected by Frisch & Kalb (2006) for a group of species with complex columella previously placed in *Ocellularia* and *Myriotrema* (Hale 2980). The morphological distinction between *Stegobolus* and two further genera with complex columella, *Melanotrema* and *Redingeria* (Frisch & Kalb 2006), proved difficult. Molecular phylogenetic analysis, however, showed that the genera are well separated phylogenetically and also that *Stegobolus* sensu Frisch & Kalb (2006) forms two separate lineages with are not closely related, *Stegobolus* s.str. and *Rhabdodiscus* (Rivas Plata *et al.* 2012b), the latter corresponding to the *S. auberianus* group as defined by Frisch & Kalb (2006). Since it is yet unclear to which lineage the unsequenced species belong, we are here treating *Stegobolus* in a wide sense, including also the species belonging in *Rhabdodiscus*. Species of *Stegobolus* s.str. appear to have apothecia with mostly uncarbonized excipulum, whereas in species of *Rhabdodiscus*, the excipulum is generally carbonized.

Key to the species of *Stegobolus* found or expected in Costa Rica (18)

1. Excipulum and columella uncarbonized except sometimes for apical portion, pale to dark brown; apothecial margin thick, usually recurved and exposing inner, felty-pruinose surface 2
- Excipulum and columella carbonized; apothecial margin not thickened, inclined to recurved 5

2. Ascospores submuriform ..... ***S. wrightii***
- Ascospores transversely septate 3

3. Columella forming distinctly radiating strands ..... ***S. radians***
- Columella irregular, not radiating 4

4. Schizidia frequently present ..... ***S. berkeleyanus***
- Schizidia absent ..... ***S. anamorphus***

5. Ascospores colourless, transversely septate only 6
- Ascospores grey-brown, transversely septate to submuriform 14

6. Psoromic acid 7
- Chemistry variable but lacking psoromic acid 11

7. Ascospores 7–13-septate, 25–35 µm long ..... ***S. emersus***
- Ascospores 3–5(–7)-septate, 15–25 µm long 8

8. Upper part of apothecia including columella with salmon-colored pigment ..... ***S. lankaensis***
- Apothecia lacking pigment 9

9. Isidia present ..... ***S. isidiiferus***
- Isidia absent 10

10. Thallus more or less verrucose; columella remaining entire ..... ***S. granulosus***
- Thallus smooth to uneven; columella breaking into 2–5 teeth ..... ***S. subcavatus***

11. Apothecia broadly chroodiscoid, up to 3.5 mm diam.; columella both radiating and forming concentric layers, mottled with orange pigment; thallus olive-brown; no substances ..... ***S. percolumellatus***
- Apothecia not chroodiscoid, up to 2 mm diam.; irregular to radiating but not forming concentric layers, lacking pigmentation; thallus olive-green; hypoprotocetraric acid or cinchonarum or reconditus unknown 12

12. Reconditus unknown; columella broad-stump-shaped ..... ***S. reconditus***
- Hypoprotocetraric acid or cinchonarum unknown; columella reticulate-radiate 13

13. Hypoprotocetraric acid; schizidia often present ..... ***S. actinotus***
- Cinchonarum unknown; schizidia absent ..... ***S. subemersus***

14. Ascospores transversely septate 15
- Ascospores submuriform 16

15. Columella lobate with broad-stump-shaped central part ..... ***S. auberianus***
- Columella reticulate-radiate with narrow central part ..... ***S. anamorphoides***

16. Lichexanthone; apothecia often becoming irregular to lirelliform ..... ***S. metaphoricus***
- Psoromic acid; apothecia rounded to angular 17

17. Columella lobate with broad-stump-shaped central part ..... ***S. crassus***
- Columella reticulate-radiate with narrow central part ..... ***S. fissus***

Stegobolus actinotus (Tuck.) Frisch & Kalb

Stegobolus actinotus (Tuck.) Frisch & Kalb, Biblioth. Lichenol. 92: 429 (2006); *Thelotrema actinotum* Tuck., Proc. Amer. Ac. Arts Sci. 5: 411 (1862); *Ocellularia actinota* (Tuck.) Müll. Arg., Flora 70: 397 (1887). Holotype. Cuba, *Wright s.n.* (FH!; Wright, Lich. Cubae 132; isotype: H-NYL 22643!, L!, M!).

Thallus grey-olive-yellow, smooth to uneven, producing schizidia, with dense, prosoplectenchymatous cortex with internal splitting; schizidia rounded to irregular, 0.1–0.2 mm diam.; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia sessile, angular-rounded to irregular, 0.6–2 mm diam.; disc partially covered by 0.4–1 mm wide pore, flesh-colored, partially filled by white-pruinose columella; margin entire to fissured, brown-black, felty white-pruinose. Columella present, reticulate-radiate, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 90–120 µm

high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–7-septate, 11–21 × 5–6 µm, fusiform, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids.

Remarks:—*Stegobolus actinotus* is one of three species in the genus known to form schizidia and the only species producing hypoprotocetraric acid as secondary substance. It is otherwise most similar to *S. subemersus* (see below), which lacks schizida and contains the cinchonarum unknowns.

Specimens examined:—The species is not yet known from Costa Rica, but has been reported from Panama (Hale 1978).

Stegobolus anamorphoides* (Nyl.) Lücking, *comb. nov. (Fig. 29A–B)
MycoBank #800229

Thelotrema anamorphoides Nyl., Flora 52: 120 (1869); *Phaeotrema anamorphoides* (Nyl.) Müll. Arg., J. Linn. Soc. London 30: 451 (1895); *Rhabdodiscus anamorphoides* (Nyl.) Vain., Ann. Acad. Sci. Fenn., Ser. A, 15(6): 184 (1921). Brazil, *Glaziou 1906* (M!; isotypes: G!, H-NYL 22688!).
Phaeographis chionodiscus Redinger, Arkiv Bot. 27A: 72 (1935). Holotype. Brazil, *Malme 3559* (S!).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia sessile, angular-rounded, 1–3 mm diam.; disc partially covered by 0.5–2 mm wide pore, partly filled by brown-black, white-pruinose columella; margin fissured to lobulate, brown-black, felty white-pruinose. Columella present, lobate-reticulate, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 4–8/ascus, 3–5-septate, 10–15 × 6–8 µm, ellipsoid, with thick septa and lens-shaped lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—*Stegobolus anamorphoides* belongs to the core group of the *Rhabdodiscus* clade which also includes *S. crassus* and *S. fissus*, all characterized by a carbonized excipulum and columella and psoromic acid as secondary substance. Among the species with brown, transversely septate ascospores, *S. anamorphoides* is characterized by its columella becoming reticulate and lacking a broad-stump-shaped central part. Most similar is *S. auberianus* (see below), which has a broad-stump-shaped to lobate columella.

Specimens examined:—COSTA RICA. Puntarenas: Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), fully shaded; Feb 1997, *Lücking 97-244* (CR), *97-247* (F, CR, USJ).

***Stegobolus anamorphus* (Nyl.) Frisch & Kalb** (Fig. 29C)

Stegobolus anamorphus (Nyl.) Frisch & Kalb, Biblioth. Lichenol. 92: 431 (2006); *Thelotrema anamorphum* Nyl., Acta Soc. Sci. Fenn. 7: 452 (1863); *Ocellularia anamorpha* (Nyl.) Riddle, Mycologia 4: 126 (1912). Holotype. French Guiana, *Leprieur 1276* (H-NYL 22610!; isotype: G!).

Thallus light grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia sessile, angular-rounded to irregular, 1–3.5 mm diam.; disc partially covered by 0.5–2.5 mm wide pore, flesh-colored, partly filled by white-pruinose columella; margin entire to fissured, brown-black, felty white-pruinose. Columella present, reticulate, brown. Excipulum prosoplectenchymatous, pale brown; periphysoids absent. Hymenium 100–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–7-septate, 14–20 × 5–7 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

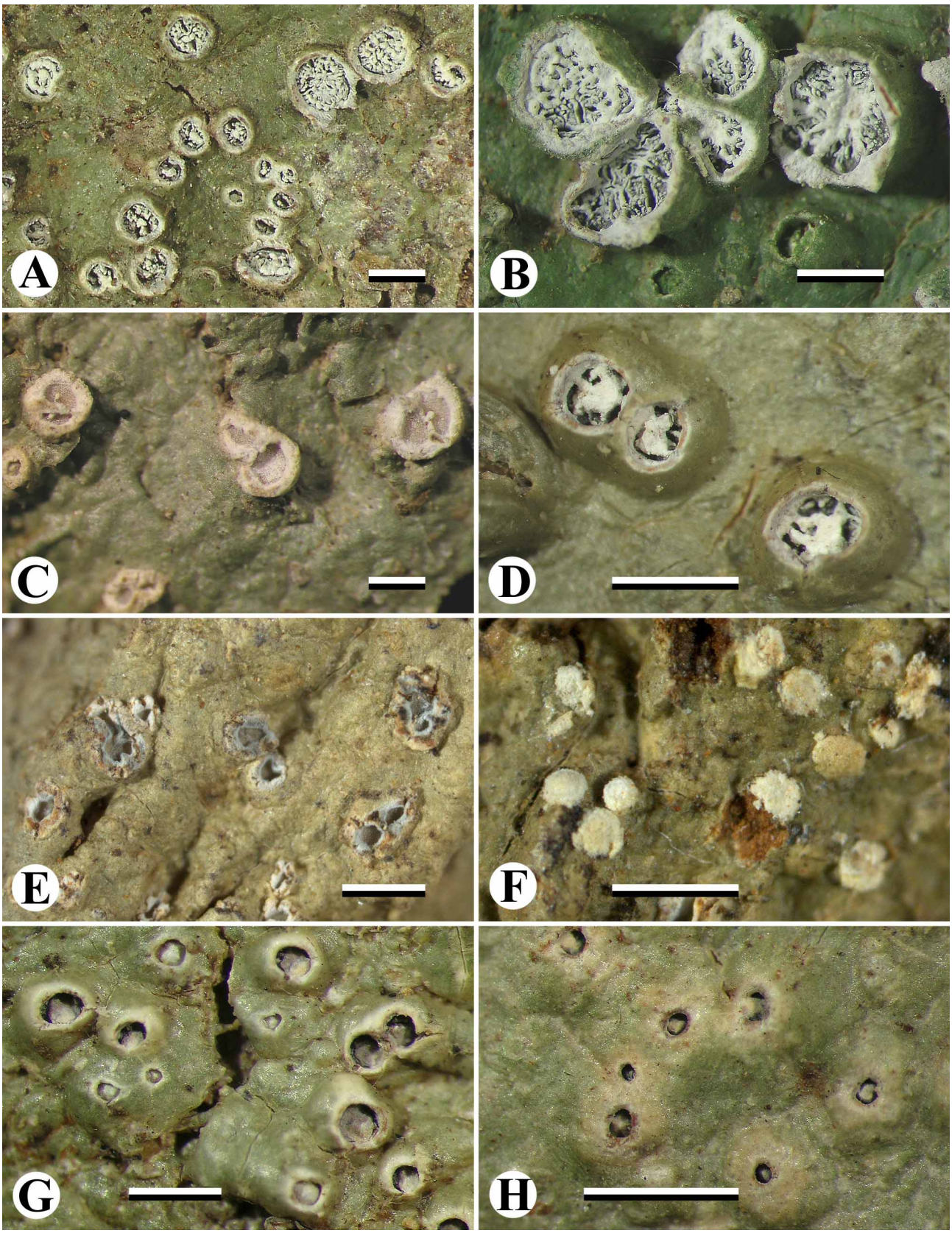

FIGURE 29. *A–B. Stegobolus anamorphoides*. C. *Stegobolus anamorphus*. D. *Stegobolus auberianus*. E–F. *Stegobolus berkeleyanus*. G. *Stegobolus crassus*. H. *Stegobolus emersus*. Scale = 1 mm.

Remarks:—This species is very similar and closely related to *Stegobolus wrightii* (see below) and differs only in the transversely septate versus submuriform ascospores. Both species belong to the core group of *Stegobolus* s.str., characterized by uncarbonized excipula and columellae and a rather broad apothecial margin. *Ocellularia subwrightii* Hale is usually considered a synonym of *S. anamorphus*, but the type of that species differs in having a salmon-colored apothecial pigment.

Specimens examined:—The species is not yet known from Costa Rica, but has been reported from Panama (Hale 1978).

***Stegobolus auberianus* (Mont.) Frisch & Kalb** (Fig. 29D)

Stegobolus auberianus (Mont.) Frisch & Kalb, Biblioth. Lichenol. 92: 433 (2006); *Thelotrema auberianum* Mont. in Sagra, Hist. de l'Ile Cuba, Bot.: 163 (1838–1842); *Ocellularia auberiana* (Mont.) Hale, Mycotaxon 11: 136 (1980). Holotype. Cuba, *Auber s.n.* (H-NYL 22615!).

Thelotrema glyphidellum Stirt., Proc. Philos. Soc. Glasgow 10: 161 (1876); *Phaeotrema glyphidellum* (Stirt.) Zahlbr., Cat. Lich. Univ. 2: 607 (1923); *Phaeotrema glyphicum* var. *glyphidellum* (Stirt.) Redinger, Arkiv Bot. 28A(8): 73 (1936). Holotype. Brazil, *Trail s.n.* (BM!).

Phaeotrema virens Müll. Arg., Flora 70: 398 (1887); *Ocellularia virens* (Müll. Arg.) Hale, Mycotaxon 11: 138 (1980). Holotype. Brazil, *Puiggari 3052* (G!).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia sessile, angular-rounded to irregular, 1–3 mm diam.; disc partially covered by 0.5–2 mm wide pore, partly filled by brown-black, white-pruinose columella; margin fissured, brown-black, felty white-pruinose. Columella present, broad-stump-shaped to lobate, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 4–8/ascus, 3–7-septate, 12–20 × 5–8 µm, ellipsoid, with thick septa and lens-shaped lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This is one of five species in the *Stegobolus auberianus* group (*Rhabdodiscus*) with psoromic acid and grey-brown, transversely septate ascospores. The species differ mainly in the shape of their columellae: broad-stump-shaped in '*Phaeotrema*' *jamaicense* Müll. Arg., which also has a finely verrucose thallus, fissured in '*Phaeotrema caracasanum*' Müll. Arg., lobate with broad center in *S. auberianus* and *S. tanzanicus* Frisch (which produces isidia), and reticulate with narrow center in *S. anamorphoides* (see above). The latter was synonymized with *S. auberianus* by Frisch & Kalb (2006) but is here kept separate on account of the differently shaped columella.

Specimens examined:—COSTA RICA. Alajuela: San Ramón Forest Reserve, near house at Río Lorencito, 5 km NE of Cerro Jabonal; 10° 13' N, 84° 37' W, 1000 m; humid, mossy forest with many ferns on mountain ridge, on thin trunk in undergrowth; Nov 1988, *Sipman et al. 41990* (B, CR), *41992* (B, CR). Limón: Bananal and jungle at Hamburg Farm; 20–30 m; Mar 1930, *Dodge & Nevermann 8313* (FH; as *Ocellularia auberianoides* (Nyl.) Müll. Arg.). Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, second part of trail from Los Patos to Sirena station; 83° 33' W, 8° 32' N, sea level; lowland rain forest zone, oldgrowth secondary forest and closed secondary vegetation, on bark (lower stem), semi-exposed; Apr 2003, *Sipman 51103f* (B, INB). Finca Quebrada Bonita-Garabú, La Fila; 83° 35' W, 9° 34' N, 0–100 m; Nov 2008, *Chaves 3292*, *3312* (INB). Las Cruces Biological Station, San Vito de Coto Bruz; 8° 47' N, 82° 58' W, 1200 m; on ridge beyond Rio Java, on trunks and undergrowth of disturbed primary forest; Oct 2004, *Sipman 53259* (B, INB).

***Stegobolus berkeleyanus* Mont** (Fig. 29E–F)

Stegobolus berkeleyanus Mont. in Hook., London J. Bot. 4: 4 (1845); *Ocellularia berkeleyana* (Mont.) Zahlbr., Cat. Lich. Univ. 2: 584 (1923). Holotype. Philippines, *Cuming 2185* (PC!; isotypes: BM!, G!).
Byssophytum album Groenh., Nederlandsch. Kruidkundig Archief 46: 783 (1936). Lectotype (Frisch & Kalb 2006: 443). Indonesia, *Groenhart 576* (L!).
Thelotrema leucotylium Nyl., Bull. Soc. Linn. Normandie, Sér. 2, 7: 166 (1874); *Ocellularia leucotyla* (Nyl.) Müll. Arg., Bull. Soc. Roy. Bot. Belgique 30: 51 (1891). Holotype. India, *Kurz 101* (M!; isotypes: BM!; H-NYL 22686!; UPS!).

Thallus grey-olive, smooth to uneven, producing schizidia, with dense, prosoplectenchymatous cortex; schizidia prominent, 0.5-1 mm diam.; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia sessile, angular-rounded, 0.5–2 mm diam.; disc exposed, flesh-colored, partly filled by white-pruinose columella; margin fissured to lobulate, pale brown, felty white-pruinose. Columella present, reticulate, pale brown. Excipulum prosoplectenchymatous, brown; periphysoids absent. Hymenium 80–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–5-septate, 12–22 × 5–7 µm, fusiform, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—The type species of *Stegobolus* is characterized by apothecia and ascospores similar to those of *S. anamorphus* (see above), but differs from the latter in the formation of schizidia on the thallus. The species is often sterile and may then be confused with other species of the family producing schizidia. However, most of these have a different chemistry: stictic acid and in part lichexanthone in *Chapsa calathiformis* (Vain.) Lumbsch & Papong and *Myriotrema frondosolucens* (see above), hypoprotocetraric acid in *Myriotrema neofrondosum* and *Stegobolus actinotus* (see above), and cinchonarum unknown in '*Stegobolus montagnei* Frisch & Emmerer' (ined.; Frisch & Kalb 2006). The only other known species with schizidia and psoromic acid is *Myriotrema frondosum* Hale, which has a different type of apothecia and in sterile condition can be separated from *Stegobolus berkeleyanus* by the different ontogeny of the schizidia, which are not prominent as in the latter.

Specimens examined:—The species is not yet known from Costa Rica, but has been reported from Panama (Hale 1978).

***Stegobolus crassus* (Müll. Arg.) Frisch** (Fig. 29G)

Stegobolus crassus (Müll. Arg.) Frisch, Bibl. Lichenol. 92: 448 (2006); *Leptotrema crassum* Müll. Arg., Flora 65: 332 (1882). Lectotype (Hale 1981: 302): Indonesia (Java), *Junghuhn 158* (L!; isolectotype: G!).
Leptotrema fallax Müll. Arg., Flora 70: 62 (1887). Holotype. Australia, *Hodkinson s.n.* (G!; isotype: M!).
Leptotrema sandwicense Zahlbr., Ann. Mycol. 10: 372 (1912). Lectotype (Hale 1981: 307): U.S.A. (Hawaii), *Rock 60* (W!).
Leptotrema oleosum Zahlbr., Bot. Magaz. Tokyo 41: 317 (1927). Holotype. Japan, *Faurie 2415* (W!).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, angular-rounded, 1–2.5 mm diam.; disc partially covered by 0.5–1.5 mm wide pore, partly filled by brown-black, white-pruinose columella; margin fissured, brown-black, white-pruinose. Columella present, broad-stump-shaped to lobate, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–1 longitudinal septa per segment, 12–19 6–8 µm, ellipsoid, with thick septa and rounded lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—The concept of *Stegobolus crassus*, which belongs to the core of the *S. auberianus* group (*Rhabdodiscus*), is confusing in the literature. At some point, all forms with complex columella, submuriform brown ascospores, and psoromic acid were subsumed under this epithet, including *S. fissus* and other similar

taxa (Mangold *et al.* 2009). However, close examination showed that species within this complex can be distinguished by the development and shape of their columellae, and hence we do not only agree with Frisch & Kalb (2006) that *S. fissus* should be kept separate but also further species must be distinguished: *Thelotrema cubanum* Tuck., with broad-stump-shaped, entire columella that completely fills the disc to the margin, *Stegobolus crassus* with lobate columella with broad-stump-shaped center, *Thelotrema epitrypum* Nyl., with similar columella as in *S. crassus* but producing isidia, *Leptotrema integrum* Müll. Arg., with fissured columella, *Ocellularia marivelensis* (see above under *Redingeria microspora*), with fissured columella and grainy thallus surface due to columnar clusters of calcium oxalate crystals, *Trypethelium schizostomum* Leight., with reticulate columella with narrow center, *Thelotrema inalbescens* Nyl., with reticulate columella and white thallus, and *Stegobolus fissus* (see below) with radiate columella similar to that of *S. radians* (see below).

Specimens examined:—COSTA RICA. Guanacaste: Barra Honda National Park, Barra Honda Biological Station (Tempisque Conservation Area), Barra Honda Mountains, 140 km WNW of San José, 10 km ENE of Nicoya, main trail to Terciopelo cave and Mirador; 85° 21' W, 10° 10' N, 400–500 m; lowland to lower montane moist forest zone, disturbed primary and oldgrowth secondary forest with calcareous rock outcrops, on bark (lower trunk), partially shaded; Mar 2004, *Lücking 17542* (CR, F, INB, USJ). Puntarenas: Las Tablas Protection Zone, La Neblina Section (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km ENE of San Vito near Las Mellizas, access road to fincas; 82° 45' W, 8° 55' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower trunk), semi-exposed; Jun 2002, *Lücking 15102b*, *15103b* (F).

***Stegobolus emersus* (Kremp.) Frisch & Kalb** (Fig. 29H)

Stegobolus emersus (Kremp.) Frisch & Kalb, Biblioth. Lichenol. 92: 452 (2006); *Thelotrema emersum* Kremp., Flora 59: 221 (1876); *Ocellularia emersa* (Kremp.) Müll. Arg., Flora 69: 310 (1886); *Phaeotrema emersum* (Kremp.) Zahlbr., Denkschr. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 83: 119 (1909). Holotype. Brazil, *Glaziou 3189* (M!; isotypes: G!, H-NYL 22435!, UPS!, W!).

Thallus grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.4–0.8 mm diam.; disc partially covered by 0.2–0.4 mm wide pore, partly filled by brown-black, white-pruinose columella; margin fissured, brown-black, felty white-pruinose. Columella present, broad-stump-shaped to lobate, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 100–130 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 7–13-septate, 25–35 × 5–6 µm, fusiform, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This species belongs in the *Stegobolus granulosus* complex with carbonized excipula and columellae, colorless transversely septate ascospores, and psoromic acid. It differs from most other species in this complex in the relative longer ascospores with more numerous septa. Similarly long and multiseptate ascospores are found in *S. schizostomus* (Tuck.) Frisch, with reticulate columella with narrow center.

Specimens examined:—COSTA RICA. Alajuela: Río Frío; 84° 43' W, 10° 56' N, 0–100 m; regenerating forest patch; Feb 2009, *Chaves 3505*, *3519*, *3535* (INB). Limón: Hitoy Cerere Biological Reserve, Hitoy Cerere Biological Station (La Amistad Caribe Conservation Area), Talamanca Ridge, 125 km ESE of San José, 40 km S of Limón, near Pandora, trails through forest above station (Sendero Espavel and Sendero Tepesquintle); 83° 02' W, 9° 40' N, 150–300 m; lowland to lower montane rain forest zone, partly disturbed primary forest, on bark (lower trunk), partially shaded; Mar 2004, *Sipman 51637* (B, INB). Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, round trail NW of station (Sendero Sirena and Sendero

Guanacaste); 83° 35' W, 8° 29' N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (lower stem), partially shaded; Apr 2003, *Lücking 16234b* (F).

***Stegobolus fissus* (Nyl.) Frisch & Kalb** (Fig. 30A)

Stegobolus fissus (Nyl.) Frisch in Frisch & Kalb, Biblioth. Lichenol. 92: 455 (2006); *Thelotrema fissum* Nyl., Ann. Sci. Nat. Bot., Sér. 4, 11: 258 (1859); *Leptotrema fissum* (Nyl.) Müll. Arg., Flora 65: 333 (1882); *Rhabdodiscus fissus* (Nyl.) Vain., Ann. Acad. Sci. Fenn., Ser. A 15(6): 184 (1921); *Ocellularia fissa* (Nyl.) Hale, Mycotaxon 11: 136 (1980). Lectotype (Hale 1974: 40). Réunion, *Richard s.n.* (H-NYL 22696!; isolectotype: G!).

Thallus light grey-olive-yellow, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, angular-rounded, 0.6–1.8 mm diam.; disc partially covered by 0.2–1 mm wide pore, partly filled by brown-black, white-pruinose columella; margin fissured, brown-black, white-pruinose. Columella present, radiate, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 90–110 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3–7 transverse septa and 0–1 longitudinal septa per segment, 12–22 × 6–11 µm, ellipsoid, with thick septa and rounded lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This species has been subsumed under *S. crassus* by Mangold *et al.* (2009); Frisch & Kalb (2006) kept it separate from *S. crassus* but included a large number of synonyms. However, the columella of *S. fissus* is radiate from the beginning, lacking a broad-stump-shaped center, and thus different from all other taxa in this complex.

Specimens examined:—COSTA RICA. Guanacaste: Barra Honda National Park, Barra Honda Biological Station (Tempisque Conservation Area), Barra Honda Mountains, 140 km WNW of San José, 10 km ENE of Nicoya, main trail to Terciopelo cave and Mirador; 85° 21' W, 10° 10' N, 400–500 m; lowland to lower montane moist forest zone, disturbed primary and oldgrowth secondary forest with calcareous rock outcrops, on bark (lower trunk), semi-exposed; Mar 2004, *Sipman 52043* (B, INB). Puntarenas: Las Tablas Protection Zone, Los Portones Section (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km ENE of San Vito, 5 km on gravel road from Progreso to Las Tablas, roadside; 82° 48' W, 8° 55' N, 1600 m; montane rain forest zone, abandoned roadside pasture with dense shrubs and treelets, on bark (lower trunk), semi-exposed; Jun 2002, *Sipman 47951* (B, INB).

***Stegobolus granulosus* (Tuck.) Frisch** (Fig. 30B)

Stegobolus granulosus (Tuck.) Frisch in Frisch & Kalb, Biblioth. Lichenol. 92: 460 (2006); *Thelotrema granulosum* Tuck., Amer. J. Arts Sci., Ser. 2(25): 426 (1858); *Thelotrema* '*granularis*' Müll. Arg., Hedwigia 32: 131 (1893) [orth. error]; *Ocellularia granulosa* (Tuck.) Zahlbr., Cat. Lich. Univ. 2: 591 (1923). Lectotype (Frisch & Kalb 2006: 460). U.S.A., *Hale s.n.* (FH!; isolectotype: M!).

Thelotrema efformatum Kremp., Flora 59: 221 (1876); *Ocellularia efformata* (Kremp.) Zahlbr., Cat. Lich. Univ. 2: 590 (1923). Holotype. Brazil, *Glaziou 3190* (M!; isotypes: G!, H-NYL 22434!, UPS!).

Thelotrema schizostomum Kremp., Flora 59: 222 (1876) [nom. illegit., non *Thelotrema schizostomum* Tuck.]; *Ocellularia emersella* Müll. Arg., J. Linn. Soc. London, Bot. 30: 453 (1895); *Thelotrema emersellum* (Müll. Arg.) Vain., Cat. Welwitsch. African Plants 2: 429 (1901); *Ocellularia krempelhuberi* Zahlbr., Cat. Lich. Univ. 2: 593 (1923) [nom. nov. superfl.]. Holotype. Brazil, *Glaziou 3260* (M!; isotypes: B!, G!, H-NYL 22436!, UPS!).

Thelotrema granulatulum Nyl., Flora 59: 561 (1876); *Ocellularia granulatula* (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 592 (1923); *Rhabdodiscus granulatulus* (Nyl.) Vain., Ann. Acad. Sci. Fenn., ser. A 15(6): 184 (1921). Holotype. Cuba, *Wright 68* (H-NYL 22611b!).

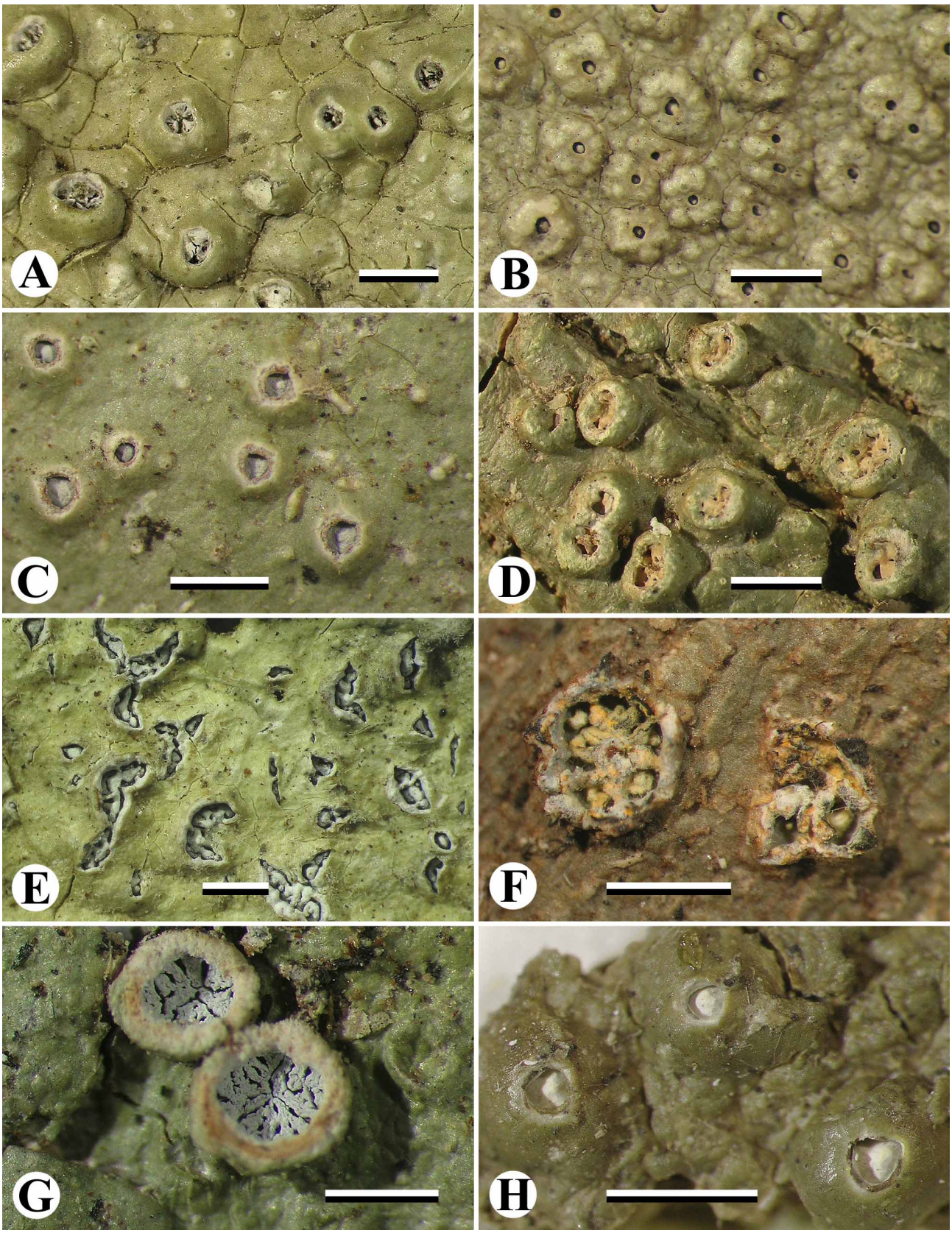

FIGURE 30. A. *Stegobolus fissus*. B. *Stegobolus granulosus*. C. *Stegobolus isidiiferus*. D. *Stegobolus lankaensis*. E. *Stegobolus metaphoricus*. F. *Stegobolus percolumellatus*. G. *Stegobolus radians*. H. *Stegobolus reconditus*. Scale = 1 mm.

Thallus light grey-olive, smooth to uneven or densely verrucose, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, angular-rounded, 0.4–1 mm diam.; disc partially covered by 0.2–0.6 mm wide pore, partly filled by brown-black, white-pruinose columella; margin fissured, brown-black, felty white-pruinose. Columella present, broad-stump-shaped to reticulate, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 100–130 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–7-septate, 15–30 × 5–8 µm, fusiform, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This is the most common species of the *S. auberianus* group (*Rhabdodiscus*); it forms the center of the species with colorless, transversely septate ascospores. Also in this complex, species are distinguished by the shape and development of their columellae: broad-stump-shaped to lobate in *S. granulosus*, similar but with isidia in *S. isidiiferus* (see below), similar but with salmon-colored pigment in *S. lankaensis* (see below), fissured in *S. subcavatus* (see below), and reticulate with narrow center in *S. schizostomus* (Tuck.) Frisch. *Stegobolus emersus* (see above) and related species exhibit a similar variation but have longer ascospores with more numerous septa. The thallus of *S. granulosus* is either densely verrucose with rather thick apothecial margins or smooth to uneven with thinner, often fissured apothecial margins. Both forms have been found in Florida and in Costa Rica. If they turn out to be specifically different in future studies using molecular methods, the epithets *granulosus* and *granulatum* would cover the verrucose form and the epithets *efformatum* and *emersella* the smooth form.

Specimens examined:—COSTA RICA. Cartago: CATIE agricultural research centre near Turrialba, Los Espaveles trail; 9° 55' N, 83° 40' W, 600 m; epiphytic in undergrowth of primary forest on steep slope along river; Nov 1988, *Sipman & Döbbeler 42394* (B, CR). Limón: Hitoy Cerere Biological Reserve, Hitoy Cerere Biological Station (La Amistad Caribe Conservation Area), Talamanca Ridge, 125 km ESE of San José, 40 km S of Limón, near Pandora, trail along Río Estrella to waterfall; 83° 02' W, 9° 40' N, 150 m; lowland to lower montane rain forest zone, secondary vegetation and disturbed primary forest along river, on bark (lower trunk), fully shaded; Mar 2004, *Sipman 51637* (B, INB). Jungle in Riotte Purchase; 20–30 m; Mar 1930; *Dodge & Nevermann 7845*, *7848* (FH). Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, second part of trail from Los Patos to Sirena station; 83° 33' W, 8° 32' N, sea level; lowland rain forest zone, oldgrowth secondary forest and closed secondary vegetation, on bark (lower trunk), partially shaded; Apr 2003, *Grube 11477* (GZU, INB); ibid., round trail NW of station (Sendero Sirena and Sendero Guanacaste); 83° 35' W, 8° 29' N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (vine), fully shaded; Apr 2003, *Lücking 16243b* (F, INB). Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), fully shaded; Feb 1997, *Lücking 97-107*, *108a*, *97-142*, *97-177* (F). On road to San Vito, 3.5 km SE of Paso Real on Río Grande de Terraba; 9° 00' N, 83° 15' W, 500 m; tropical moist forest zone, epiphyte in secondary forest; Dec 1978, *Sipman 11815* (U).

***Stegobolus isidiiferus* (Hale) Frisch** (Fig. 30C)

Stegobolus isidiiferus (Hale) Frisch, Biblioth. Lichenol. 92: 467 (2006); *Ocellularia isidiifera* Hale, Phytologia 27: 492 (1974). Holotype. Panama, *Hale 38709* (US!).

Thallus light grey-olive-yellow, smooth to uneven, producing isidia, with dense, prosoplectenchymatous cortex with internal splitting; isidia cylindrical, erect to decumbent, up to 1 mm long and 0.1–0.15 broad; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, angular-rounded, 0.6–1 mm diam.; disc partially covered by 0.3–0.5 mm wide pore, partly filled by brown-black,

white-pruinose columella; margin fissured, grey-brown, white-pruinose. Columella present, broad-stump-shaped to reticulate, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 90–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–7-septate, 17–25 × 6–7 µm, fusiform, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This species agrees with forms of *Stegobolus granulosus* with smooth thallus but can be distinguished by the conspicuous isidia. Several other species of *Stegobolus* produce similar isidia but can be distinguished by lack of excipular carbonization or by pigmented ascospores (Frisch & Kalb 2006).

Specimens examined:—COSTA RICA. Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, round trail NW of station (Sendero Sirena and Sendero Guanacaste); 83° 35' W, 8° 29' N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (lower stem), partially shaded; Apr 2003, *Lücking 16217* (F, INB); ibid., on bark (lower stem), fully shaded; Apr 2003, *Lücking 16248* (F, INB).

Stegobolus lankaensis* (Hale) Lücking, *comb. nov. (Fig. 30D)
MycoBank #800060

Ocellularia lankaensis Hale, Bull. Brit. Mus. Nat. Hist., Bot. Ser., 8: 309 (1981). Holotype. Sri Lanka, *Hale 47184* (US!; isotype: BM!).

Thallus light grey-green, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, angular-rounded, 1–1.3 mm diam.; disc covered by narrow, 0.2–0.3 mm wide pore, filled by brown-black, salmon-pruinose columella; margin entire, grey-brown, salmon-pruinose. Columella present, broad-stump-shaped, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–110 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 5–7-septate, 10–22 × 5–7 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids (P+ yellow); salmon pigment on apothecial disc and columella.

Remarks:—This species is most similar to *Stegobolus granulosos* (see above) but differs in the salmon-colored pigment of the apothecia. A similar difference is found between *S. anamorphus* (see above) and *S. subwrightii*.

Specimens examined:—COSTA RICA. Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, round trail NW of station (Sendero Sirena and Sendero Guanacaste); 83° 35' W, 8° 29' N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (lower trunk), partially shaded; Apr 2003, *Lücking 16236b* (CR, F, USJ).

***Stegobolus metaphoricus* (Nyl.) Frisch** (Fig. 30E)

Stegobolus metaphoricus (Nyl.) Frisch, Biblioth. Lichenol. 92: 470 (2006); *Thelotrema metaphoricum* Nyl., Acta Soc. Sci. Fenn. 7: 455 (1863); *Ocellularia metaphorica* (Nyl.) Hale, Mycotaxon 11: 137 (1980). Holotype. Colombia, *Lindig 2814* (H-NYL 22695!; isotypes: B!, BM!, FH!, G!, H-NYL 22524!, M!, S!, UPS!).

Thallus light yellow-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia sessile, angular to lirellate, 0.5–3 ×

0.5–1.8 mm large; disc partially covered by 0.3–1 mm wide pore, partly filled by brown-black, white-pruinose columella; margin fissured, brown-black, felty white-pruinose. Columella present, reticulate, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched; hymenium inspersed. Ascospores 8/ascus, 10–17 × 5–8 µm, ellipsoid, with thick septa and rounded lumina, brown, young I+ violet-blue (amyloid), submuriform. Secondary chemistry: lichexanthone.

Remarks:—*Stegobolus metaphoricus* is a very characteristic species, distinguished from all other species of the genus by the combination of elongate-lirellate, carbonized apothecia and lichexanthone. *Leptotrema microsporum* Zahlbr. [≡ *Thelotrema microsporoides* Zahlbr.] was placed in synonymy with *S. metaphoricus* by Frisch & Kalb (2006), but differs in the verrucose, grey rather than yellow-green thallus and the rounded apothecia; it actually belongs in the genus *Redingeria* (see above).

Specimens examined:—COSTA RICA. Cartago: Gorge of Río Pejivalle; 600–650 m; Sep 1929; *Dodge & Thomas s.n.* (FH; as *Phaeotrema auberianum* (Mont.) Müll. Arg.). Guanacaste: Lomas de Barbudal Biological Reserve, Lomas de Barbudal Station (Tempisque Conservation Area), Río Tempisque Bassin, 140 km WNW of San José and 20 km WSW of Bagaces, trail from station to Río Barbudal; 85° 22' W, 10° 30' N, 100 m; lowland to lower montane moist forest zone, disturbed gallery forest and forest remnants, on bark (lower stem), semi-exposed; Mar 2003, *Sipman 51043* (B, CR). Palo Verde National Park, Palo Verde Station (Tempisque Conservation Area), Río Tempisque Bassin, 130 km WNW of San José and 30 km SSW of Bagaces, lower parts of Guayacan trail; 85° 21' W, 10° 21' N, 10–50 m; lowland to lower montane moist forest zone, disturbed primary forest remnants and open secondary forest, on bark (lower stem), semi-exposed; Mar 2003, *Sipman 50980a* (B, CR). Jungle between cafetal and Río San José; 480 m; Feb 1930; *Dodge & Thomas 8454* (FH). Upper portion of cañon of Río San José; 460–480 m; Feb 1930; *Dodge & Thomas 6622* (FH; as *Leptotrema microsporum* Zahlbr.). Puntarenas: Guesthouse Río Brujo, 10 km to the Rio Grande de Térraba, at the Interamerican Highway; 10° 01' N, 85° 26' W, 350 m; tropical rainforest; Jan 1979, *Kalb & Plöbst 38917*, *38923* (hb. Kalb). Las Tablas Protection Zone, Cedro Ridge, Las Alturas Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km NE of San Vito near Alturas, surroundings of station and trail into forest; 82° 50' W, 8° 57' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower stem), fully shaded; Jun 2002, Lücking 15077c (F, INB); ibid., pasture with group of trees bordering forest, on bark (lower trunk), semi-exposed; Jun 2002, *Sipman 47818f* (B, INB); ibid., La Neblina Section (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km ENE of San Vito near Las Mellizas, access road to fincas; 82° 45' W, 8° 55' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower trunk), partially shaded; Jun 2002, *Sipman 47890f* (B, INB); ibid., Los Portones Section (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km ENE of San Vito, 5 km on gravel road from Progreso to Las Tablas, roadside; 82° 48' W, 8° 55' N, 1600 m; montane rain forest zone, abandoned roadside pasture with dense shrubs and treelets, on bark (lower trunk), semi-exposed; Jun 2002, *Sipman 47953* (B, INB). Manuel Antonio National Park, near Quepos; 9° 23' N, 84° 09' W, sea level; scattered trees around hotel at end station of bus line; Nov 1988, *Sipman 42311* (B, CR).

***Stegobolus percolumellatus* (Sipman) Frisch** (Fig. 30F)

Stegobolus percolumellatus (Sipman) Frisch, Biblioth. Lichenol. 92: 474 (2006); *Ocellularia percolumellata* Sipman, Acta Bot. Fennica 150: 170 (1994). Holotype. French Guiana, *Aptroot 15610* (B!; isotype: U, not seen).

Thallus olive-brown, smooth, with dense, prosoplectenchymatous cortex; photobiont layer with scattered clusters of calcium oxalate crystals. Apothecia erumpent to prominent, angular-rounded to irregular, 1.5–3.5 mm diam.; disc exposed, filled by brown-black, white-pruinose columella mottled with orange; margin lobulate to recurved, brown-black, felty white to orange-pruinose. Columella present, reticulate-radiate and forming concentric ridges, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent.

Hymenium 90–120 µm high, clear; paraphyses unbranched, thick. Ascospores 8/ascus, 5–9-septate, 18–28 × 5–6 µm, ellipsoid with distal ends tapering, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances; orange pigment on apothecial disc.

Remarks:—This species, which was reported from Costa Rica by Frisch & Kalb (2006), is rather unusual in the brown thallus color, lack of secondary substances in the thallus, and large apothecia that resemble those of *Gyrotrema*. It probably does not belong in *Stegobolus* s.str. or *Rhabdodiscus*.

Specimen examined:—COSTA RICA. Puntarenas: Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), fully shaded; Feb 1997, *Lücking 97-251* (F).

***Stegobolus radians* (Müll. Arg.) Frisch** (Fig. 30G)

Stegobolus radians (Müll. Arg.) Frisch, Biblioth. Lichenol. 92: 479 (2006); *Ocellularia radians* Müll. Arg., Flora 70: 397 (1887). Holotype. Brazil, *Puiggari 3049* (G!).

Ocellularia glaziovii Müll. Arg., J. Linn. Soc. London, Bot. 30: 451 (1895). Lectotype (Frisch & Kalb 2006: 481). Brazil, *Glaziou 5578* (G!; isolectotypes: BM!, M!).

Thallus light olive-green, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia sessile, angular-rounded to irregular, 1–4 mm diam.; disc partially covered by 0.5–3 mm wide pore, partly filled by brown-black, white-pruinose columella; margin fissured, dark brown, felty white-pruinose. Columella present, radiate along deep fissures in the apothecial disc, brown to dark brown. Excipulum prosoplectenchymatous, pale to dark brown; periphysoids absent. Hymenium 90–120 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 3–7-septate, 12–25 × 6–9 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—*Stegobolus radians* is closely related to *S. anamorphus* and *S. berkeleyanus* and shares with the latter the rather thick, felty pruinose apothecial margin and the uncarbonized to only partially carbonized excipulum and columella, but can be easily distinguished by the radiate columella shape along deep fissures in the apothecial disc.

Specimen examined:—COSTA RICA. Puntarenas: Cordillera de Tilarán, Monteverde, near the cheese factory; 10° 18' N, 84° 49' W, 1450 m; premontane rain forest zone, forest relics among pasturefields, on trunks; Jan 1979, *Sipman 12123* (U).

***Stegobolus reconditus* (Stirt.) Frisch** (Fig. 30H)

Stegobolus reconditus (Stirt.) Frisch, Biblioth. Lichenol. 92: 484 (2006); *Thelotrema reconditum* Stirt., Proc. Phil. Soc. Glasgow 10: 162 (1876); *Ocellularia recondita* (Stirt.) Zahlbr., Cat. Lich. Univ. 2: 600 (1923). Holotype: Brazil, *Trail s.n.* (BM!).

Thallus olive-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.5–1.1 mm diam.; disc covered by narrow, 0.2–0.3 mm wide pore, filled by brown-black, white-pruinose columella; margin entire, brown-black, white-pruinose. Columella present, broad-stump-shaped, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched, thick. Ascospores 8/ascus, 5–7-septate, 12–18 × 5–6 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: reconditus unknown.

Remarks:—This species is morphologically identical with *Stegobolus granulosus* (see above) but differs in the unknown chemical compound produced in the thallus (Frisch & Kalb 2006).

Specimens examined:—The species is not yet known from Costa Rica, but has been reported from Panama (Hale 1978).

***Stegobolus subcavatus* (Nyl.) Frisch** (Fig. 31A)

Stegobolus subcavatus (Nyl.) Frisch, Biblioth. Lichenol. 92: 491 (2006); *Thelotrema subcavatum* Nyl., Flora 59: 561 (1876); *Ocellularia subcavata* (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 601 (1923). Holotype. Lesser Antilles (St. Vincent), *Elliott 260* (TUR-VAIN 26883!; isotypes: BM!, FH!).

Thelotrema vagum Vain., J. Bot. 34: 209 (1896); *Ocellularia vaga* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 603 (1923). Holotype. Lesser Antilles (St. Vincent), *Elliott 260* (TUR-VAIN 26883!; isotypes: BM!, FH!).

Thallus olive-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia prominent, angular-rounded, 0.4–0.8 mm diam.; disc partially covered by 0.2–0.5 mm wide pore, flesh-colored, partly filled by white-pruinose columella; margin entire, brown-black, felty white-pruinose. Columella present, broad-stump-shaped to fissured, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–100 µm high, clear; paraphyses unbranched, apically capitate. Ascospores 8/ascus, 3–5-septate, 11–20 × 6–7 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—*Stegobolus subcavatus* belongs in the *Rhabdodiscus* group and differs from *S. granulosus* (see above) in the development of the columella, which ruptures early into 2–4 triangular teeth but does not become lobate or reticulate.

Specimen examined:—COSTA RICA. Puntarenas: Cordillera de Tilarán, Monteverde, near the cheese factory; 10° 18' N, 84° 49' W, 1450 m; premontane rain forest zone, forest relics among pasturefields, on trunks; Jan 1979, *Sipman 12119* (U).

***Stegobolus subemersus* (Müll. Arg.) Frisch** (Fig. 31B)

Stegobolus subemersus (Müll. Arg.) Frisch, Biblioth. Lichenol. 92: 492 (2006); *Ocellularia subemersa* Müll. Arg., Flora 69: 310 (1886). Holotype. Jamaica, *Hart comm. Joshua 125* (G!).

Thallus olive-green, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia sessile, angular-rounded, 0.5–1.8 mm diam.; disc partially covered by 0.3–1.2 mm wide pore, partly filled by brown-black, white-pruinose columella; margin fissured, brown-black, felty white-pruinose. Columella present, lobate-reticulate, carbonized. Excipulum prosoplectenchymatous, carbonized; periphysoids absent. Hymenium 80–110 µm high, clear; paraphyses unbranched, apically capitate. Ascospores 8/ascus, 3–5-septate, 11–20 × 4–6 µm, ellipsoid, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: cinchonarum unknowns.

Remarks:—This species is very similar to *Stegobolus anamorphoides* (see above) but differs in the unusual chemistry and colorless ascospores. Apart from the sterile '*S. montagnei* Frisch & Emmerer' [ined. (Frisch & Kalb 2006)], it is the only species in the genus known to contain cinchonarum unknown in the thallus.

Specimens examined:—COSTA RICA. Guanacaste: Upper portion of cañon of Río San José; 460–480 m; Feb 1930; *Dodge & Thomas 7831* (FH; as *Leptotrema wightii*).

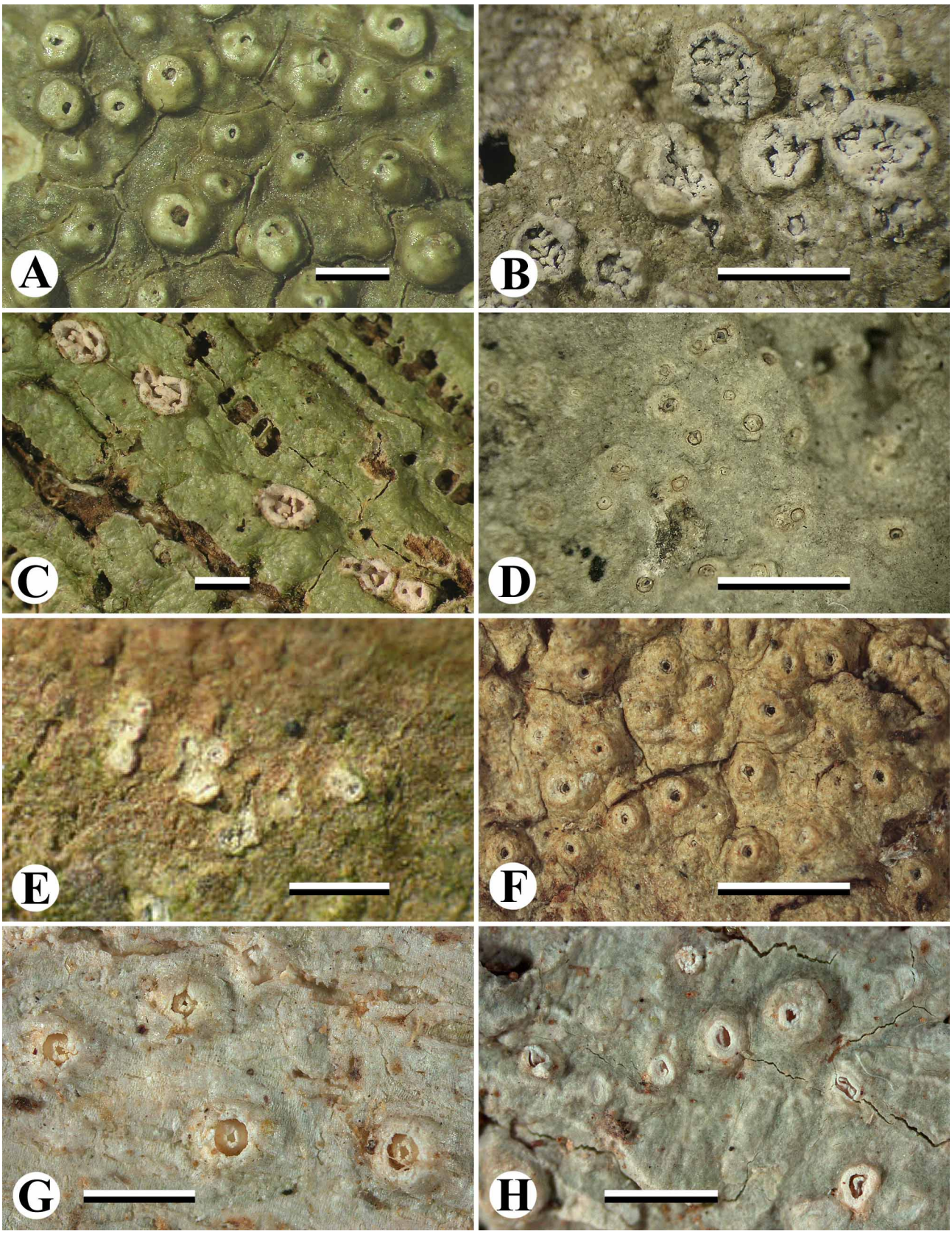

FIGURE 31. A. *Stegobolus subcavatus*. B. *Stegobolus subemersus*. C. *Stegobolus wrightii*. D. *Thelotrema adjectum*. E. *Thelotrema* aff. *adjectum*. F. *Thelotrema conveniens*. G. *Thelotrema diplotrema*. H. *Thelotrema gomeziana*. Scale = 1 mm.

***Stegobolus wrightii* (Tuck.) Frisch** (Fig. 31C)

Stegobolus wrightii (Tuck.) Frisch, Biblioth. Lichenol. 92: 496 (2006); *Thelotrema wrightii* Tuck., Proc. Amer. Acad. Arts Sci. 5: 409 (1862); *Myriotrema wrightii* (Tuck.) Hale, Mycotaxon 11: 136 (1980). Lectotype (Hale 1978: 49). Cuba, *Wright s.n.* (FH!; Wright, Lich. Cubae 143; isolectotypes: BM!, G!, H-NYL 22665!, UPS!).

Thallus light olive-green, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia sessile, angular-rounded to irregular, 1–3 mm diam.; disc partially covered by 0.5–2 mm wide pore, flesh-colored, partly filled by white-pruinose columella; margin entire, pale brown, white-pruinose. Columella present, reticulate, brown. Excipulum prosoplectenchymatous, pale brown; periphysoids absent. Hymenium 80–110 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, submuriform with 3–7 transverse septa and 0–1 longitudinal septa per segment, 12–21 × 5–8 µm, ellipsoid, with thick septa and rounded lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: psoromic, subpsoromic and 2'-*O*-demethylpsoromic acids.

Remarks:—This species is the most common of *Stegobolus* s.str. and is very close to *S. anamorphus*, being distinguished chiefly by the submuriform ascospores. *Stegobolus wrightii* typically grows on tree trunks in the understory of lowland to lower montane rain forests.

Specimens examined:—COSTA RICA. Cartago: CATIE agricultural research centre near Turrialba, Los Espaveles Trail; 9° 55' N, 83° 40' W, 600 m; epiphytic in undergrowth of primary forest on steep slope along river; Nov 1988, *Sipman & Döbbeler 42377* (B, CR). Guanacaste: Cacao Biological Station (Guanacaste Conservation area); 10° 56' N, 85° 28' W, 1000 m; epiphyte in humid primary montane forest near the station; June 1995, *Sipman 37295* (B, CR). Limón: Finca Montecristo, on Río Reventazón below Cairo; 25 m; on bark; Feb 1926; *Standley & Valerio 48501* (FH; as *Ocellularia costaricensis* Müll. Arg.). Hitoy Cerere Biological Reserve, Hitoy Cerere Biological Station (La Amistad Caribe Conservation Area), Talamanca Ridge, 125 km ESE of San José, 40 km S of Limón, near Pandora, trails through forest above station (Sendero Espavel and Sendero Tepesquintle); 83° 02' W, 9° 40' N, 150–300 m; lowland to lower montane rain forest zone, partly disturbed primary forest, on bark (lower trunk), partially shaded; Mar 2004, *Sipman 51646* (B, INB). Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, trail S of station to Río Claro; 83° 35' W, 8° 28' N, 0–100 m; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants, on bark (lower trunk), semi-exposed; Apr 2003, *Nelsen 3579b* (INB, WIS); ibid., round trail NW of station (Sendero Sirena and Sendero Guanacaste); 83° 35' W, 8° 29' N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (lower stem), semi-exposed; Apr 2003, *Grube 11491* (GZU, INB); ibid., on bark (lower trunk), partially shaded; Apr 2003, *Lücking 16236a* (CR, F, INB, USJ); ibid., Los Patos Section, Los Patos Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, access trail to station and first, hilly part (5 km) of trail to Sirena; 83° 29' W, 8° 34' N, 100–300 m; lowland rain forest zone, closed primary forest, on bark (lower stem), partially shaded; Apr 2003, *Will-Wolf 12550* (CR, INB, WIS). Finca Quebrada Bonita-Garabú, La Fila; 83° 35' W, 9° 34' N, 0–100 m; Nov 2008, *Chaves 3324* (INB). Las Cruces Biological Station, San Vito de Coto Brus; 8° 47' N, 82° 58' W, 1200 m; on ridge beyond Río Java, on trunks and undergrowth of disturbed primary forest; Oct 2004, *Sipman 53260* (B, INB). Las Tablas Protection Zone, La Neblina Section (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km ENE of San Vito near Las Mellizas, access road to fincas; 82° 45' W, 8° 55' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower trunk), partially shaded; Jun 2002, *Lücking 15101* (F, INB). Monte Verde, Cordillera de Tilaran, ca. 20 km E of Juntas; Jan 1979, *Filson 16375* (MEL).

Thelotrema Ach.

Thelotrema Ach., Meth. Lich.: 130 (1803). Type. *Thelotrema lepadinum* (Ach.) Ach.

Thallus white to yellow-grey or light olive, smooth to uneven or verrucose, ecorticate or with loose or rarely dense, proso- to paraplectenchymatous cortex; photobiont layer and medulla often with clusters of calcium oxalate crystals. Apothecia immersed to sessile, rounded to angular-rounded; disc partially covered by excipular remnants; margin entire to undulate or fissured, with distinct split between excipulum and thalline margin (double margin). Columella absent. Excipulum paraplectenchymatous, uncarbonized, colorless to brown; periphysoids present, distinct. Paraphyses unbranched. Ascospores transversely septate to muriform, fusiform-ellipsoid to oblong-cylindrical, with thin to thick septa and angular to rounded lumina and often with thick outer wall, colorless or brown, I– or I+ weakly to strongly violet-blue (amyloid). Secondary chemistry: no substances or mostly stictic or norstictic acids or relatives, rarely hypoprotocetraric acid.

Remarks:—The genus *Thelotrema* was first circumscribed in a modern sense by Frisch (2006); it is rather well-characterized by having apothecia with a double margin and periphysoids. *Thelotrema* has been shown to be monophyletic (Lumbsch *et al.* 2008; Mangold *et al.* 2008; Papong *et al.* 2009a; Rivas Plata & Lumbsch 2011a, b), with the exception of a few species with *Thelotrema*-like apothecia that fall outside the genus, such as *Chapsa platycarpa* (see above) and *Thelotrema bicinctulum* Nyl. (Rivas Plata & Lumbsch 2011a). Species of *Thelotrema* are mostly found at higher elevations and in (semi-)exposed situations and several species, including the type species, *T. lepadinum*, have close to cosmopolitan distribution ranges.

Key to the species of *Thelotrema* found or expected in Costa Rica (18)

1. Ascospores transversely septate 2
- Ascospores (sub-)muriform 8

2. Ascospores remaining colorless 3
- Ascospores becoming brown 7

3. Ascospores small, 20–45 µm long, 5–11(–15)-septate 4
- Ascospores medium-sized to large, 50–140 µm long, (11–)15–27-septate 6

4. Apothecia immersed (to erumpent), up to 0.5 mm broad; no substances ..... ***T. subtile***
- Apothecia (erumpent to) prominent, up to 0.8 mm broad; no substances or hypoprotocetraric acid 5

5. Thallus well-developed, with compacted cortex, yellow-white; no substances ..... ***T. suecicum***
- Thallus mostly endoperidermal, with loose cortex, white-grey; hypoprotocetraric acid ..... ***T. wilsonii***

6. Stictic acid ..... ***T. porinoides***
- No substances ..... ***T. diplotrema***

7. Ascospores 60–150 µm long, 15–27-septate; disc visible; thallus with loose cortex ..... ***T. lacteum***
- Ascospores 35–75 µm long, 7–15-septate; disc covered by narrow pore; thallus ecorticate ..... ***T. pachysporum***
(if ascospores smaller and stictic acid present, see *Chapsa neei* and *C. platycarpa*)

8. Ascospores remaining colorless 9
- Ascospores becoming brown 16

9. Ascospores small, 10–40 × 4–12 µm; I– 10
- Ascospores medium-sized to large, (40–)50–220 × (12–)15–40 µm, I– or mostly I+ violet-blue 13

10. No substances; ascospores 10–18 × 4–6 µm ..... ***T.* aff. *adjectum***
- Stictic acid; ascospores 15–40 × 6–12 µm 11

11. Hymenium inspersed; apothecia erumpent to prominent, to 1 mm diam.; thallus with loose cortex... ***T. gomezianum***
- Hymenium clear; apothecia immersed to erumpent, to 0.5 mm diam.; thallus with dense cortex 12

12. Ascospores 20–40 × 7–10 µm, 2.5–4 times as long as wide ..... ***T. myriocarpum***
- Ascospores 15–20 × 8–12 µm, 1.5–2.5 times as long as wide ..... ***T. submyriocarpum***

13. Ascospores (1–)2–8/ascus, 40–100(–120) × 12–25 µm 14
- Ascospores single, (80–)100–220 × (15–)20–40 µm 15

14. Apothecia immersed to erumpent, to 0.4 mm diam.; thallus more or less ecorticate; ascospores 4–8/ascus, 40–80 µm long, I–, with thin outer wall..... ***T. adjectum***
- Apothecia prominent, to 1.8 mm diam.; thallus with compacted cortex; ascospores 1–4/ascus, 65–120 µm long, I+ violet-blue, with thick outer wall ..... ***T. lepadinum***

15. Hypoprotocetraric acid ..... ***T. occlusum***
- No substances ..... ***T. conveniens***

16. Ascospores single, 150–250 × 30–35 µm; hypoprotocetraric acid..... ***T. hypoprotocetraricum***
- Ascospores (1–)2–8/ascus, 40–110 × 15–30 µm; no substances 17

17. Ascospores with thick walls and septa and rounded lumina, remaining hyaline for a long time..... ***T. lepadodes***
- Ascospores with thin walls and septa, becoming brown in early stages ..... ***T. monosporum***

***Thelotrema adjectum* Nyl.** (Fig. 31D)

Thelotrema adjectum Nyl., Flora 49: 290 (1866). Lectotype (Hale 1978: 39). Cuba, *Wright 82* (H-NYL 22572!; isolectotype: UPS!).

Thallus light grey-olive, smooth to uneven, ecorticate or with indistinct, loose cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia immersed-erumpent, rounded, 0.2–0.4 mm diam.; disc covered by narrow, 0.1–0.2 mm wide pore, barely visible; proper margin entire, yellowish white, undulate to fissured, thalline margin entire, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Paraphyses unbranched. Ascospores 4–8/ascus, 40–80 × 12–25 µm, ellipsoid, richly muriform, with thin septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Thelotrema adjectum* is a rather non-descript, probably frequently overlooked species due to its inconspicuous thallus and rather small, immersed to erumpent apothecia. Although the muriform ascospores are similar in size to those of *T. lepadinum*, the latter clearly differs in the distinctly corticate thallus, the large, prominent to sessile apothecia, and the thick-walled, amyloid ascospores.

Specimens examined:—This species is not yet known from Costa Rica but was reported from Panama (Hale 1978).

***Thelotrema* aff. *adjectum* Nyl.** (Fig. 31E)

Thallus light olive, smooth to uneven, with indistinct, loose cortex; photobiont layer with scattered clusters of calcium oxalate crystals. Apothecia immersed-erumpent, rounded, 0.2–0.3 mm diam.; disc covered by narrow, 0.05–0.1 mm wide pore, barely visible; proper margin entire, yellowish white, entire, thalline margin indistinct, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Hymenium 70–80 µm high, clear; paraphyses unbranched. Ascospores 8/ascus, 10–18 × 4–6 µm, ellipsoid, submuriform (3–5 × 0–1 septa), with thin septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—We have not yet found a name for this material which unfortunately is represented by a single, small collection only. The taxon is closest to *Thelotrema adjectum* but has much smaller ascospores. The only species in *Thelotrema* with similar ascospores and lacking secondary substances is the Indian *T. kalarense* Nagarkar, Sethy & Patw., which has much larger apothecia. The genus *Chapsa* includes some morphologically similar species, but the only species with similar ascospores and lacking secondary substances, *C. kalbii* Frisch and *C. hiata* (see above), have a whitish thallus and larger apothecia with more exposed disc, and *C. kalbii* has ascospores with thickened septa and rounded to lens-shaped lumina.

Specimens examined:—COSTA RICA. Alajuela: Volcán Tenorio National Park, Pilón Biological Station (Arenal-Tempisque Conservation Area), Tilarán Ridge, 140 km NW of San José, 25 km NNW of Tilarán, near Bijagua, main trail through forest to crater; 84° 59' W, 10° 43' N, 700–900 m; lower montane cloud forest zone, partly disturbed primary forest, on bark (lower trunk), semi-exposed; Mar 2004, *Aptroot 60508* (BR).

***Thelotrema conveniens* Nyl.** (Fig. 31F)

Thelotrema conveniens Nyl., Bull. Soc. Linn. Normand., Ser. 2, 7: 168 (1873). Lectotype (Hale 1878: 42). Colombia, *Lindig s.n.* (H-NYL 22496!).

Thallus light yellowish grey to yellowish brown, smooth to uneven, ecorticate or with indistinct, loose cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent to prominent, rounded, 0.3–0.6 mm diam.; disc partially covered by narrow, 0.2–0.3 mm wide pore; proper margin entire, yellowish white, undulate to fissured, thalline margin entire, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Paraphyses unbranched. Ascospores single, 80–200 × 20–40 µm, ellipsoid to oblong, richly muriform, with slightly thickened septa and rectangular lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Thelotrema conveniens* is rather similar to *T. adjectum* in external appearance but differs in the much larger, single ascospores which are distinctly amyloid. *Thelotrema lepadinum* can be distinguished by its much larger, prominent to sessile apothecia and ascospores occurring in numbers of 1–4 per ascus.

Specimens examined:—This species is not yet known from Costa Rica but was reported from Panama (Hale 1978).

***Thelotrema diplotrema* Nyl.** (Fig. 31G)

Thelotrema diplotrema Nyl., Ann. Sci. Nat. Bot., Ser. 4, 11: 258 (1859); *Ocellularia diplotrema* (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 588 (1923). Lectotype (Mangold *et al.*, 2009: 371). Réunion, s.col. (H-NYL 22737!).

Ocellularia turgidula Müll. Arg., J. Bot. 7: 94 (1893); *Thelotrema turgidulum* (Müll. Arg.) Hale, Mycotaxon 11: 132 (1980) [nom. illeg., non *Thelotrema turgidulum* Vain.]. Lectotype (Hale 1978: 33). New Caledonia, *Balansa s.n.* (PC!; isolectotype: G!).

Thallus light yellowish grey to light yellow-olive, smooth to uneven, with irregular, compacted cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.5–1 mm diam.; disc partially covered by 0.3–0.6 mm wide pore, brown, white-pruinose; proper margin entire, pale brown, undulate to fissured, thalline margin entire, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, pale brown; periphysoids present, distinct. Paraphyses unbranched. Ascospores 8/ascus, 50–100 × 7–13 µm, oblong with distal ends tapering, 11–19-septate, with thick septa and rounded lumina, thick-walled, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Thelotrema diplotrema* is similar and closely related to *T. lepadinum* (Lumbsch *et al.* 2008), differing mainly in the smaller, transversely septate ascospores and thus forming a sporomorph with the latter. Also similar is *T. porinoides*, which differs chiefly in producing stictic acid.

Specimens examined:—COSTA RICA. Alajuela: Volcán Tenorio National Park, Pilón Biological Station (Arenal-Tempisque Conservation Area), Tilarán Ridge, 140 km NW of San José, 25 km NNW of Tilarán, near Bijagua, access road to station and river; 84° 59' W, 10° 43' N, 700 m; lower montane cloud forest zone, exposed trees and fence posts along pasture, on bark (lower stem), partially shaded; Mar 2004, *Lücking 17220* (CR, F). Cartago: Tapantí National Park, Tapantí Section, Tapantí Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 35 km SE of San José and 18 km SE of Cartago, road above second trail to river (Sendero La Pava) below Mirador; 83° 47' W, 9° 44' N, 1700 m; montane cloud forest zone, primary forest margin along roadside, on bark (lower trunk), semi-exposed; Apr 2003, *Buck 44068* (INB, NY). Limón: Braulio Carrillo National Park, Botarrama Section (Cordillera Volcánica Central Conservation Area), Central Volcanic Ridge; 460–480 m; lower montane rain forest zone, primary forest, on bark (lower trunk), fully shaded; Apr 1991, *Lücking s.n.* (F). Puntarenas: Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), fully shaded; Feb 1997, *Lücking 97-154b* (CR), *97-171* (F). Wilson Botanical Garden, Las Cruces Biological Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 190 km SE of San José, trail beyond botanical garden; 82° 58' W, 8° 47' N, 1200 m; montane rain forest zone, primary forest, on bark (lower trunk), partially shaded; Sep 2007, *Lücking 21052* (F).

Thelotrema gomezianum* Lücking, *spec. nov. (Fig. 31H)
MycoBank #800101

Differing from *Leucodecton expallescens* in the inspersed hymenium and distinct periphysoids.

Holotype:—COSTA RICA. Puntarenas: Wilson Botanical Garden, Las Cruces Biological Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 190 km SE of San José, trail beyond botanical garden; 82° 58' W, 8° 47' N, 1200 m; montane rain forest zone, primary forest, on bark (lower trunk), partially shaded; Sep 2007, *Lücking 21085* (F).

Thallus light greyish white, smooth to uneven, with irregular, loose cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent to prominent, angular-rounded, 0.5–1 mm diam.; disc covered by 0.2–0.5 mm wide pore, brown, white-pruinose; proper margin entire, white, undulate to fissured, thalline margin entire, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, colorless to pale yellowish; periphysoids present, distinct. Paraphyses unbranched. Ascospores 8/ascus, 15–20 × 6–8 µm, ellipsoid, submuriform with 3–5 transverse septa and 0–2 longitudinal septa per segment, with thin to slighty thickened septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: stictic, constictic, hypoconstictic and cryptostictic acids.

Remarks:—This new species is dedicated to the memory of Luis Diego Gómez, Costa Rican botanist, naturalist, and conservationist. *Thelotrema gomezianum* is one of very few species in the genus with inspersed hymenium. The others are *T. oleosum* Mangold, with large, muriform ascospores and lacking secondary substances, and *T. saxicola* (Vain.) Salis., with large, muriform ascospores and psoromic acid. Other species in *Thelotrema* with small, muriform ascospores and stictic acid lack inspersion and either lack a cortex or have a dense cortex. Very similar in appearance is *Leucodecton expallescens* which, however, also lacks inspersion.

Additional specimen examined (paratype):—COSTA RICA. Puntarenas: Las Tablas Protection Zone, La Neblina Section (La Amistad Pacífico Conservation Area), Talamanca Ridge, 25 km ENE of San Vito near Las Mellizas, access road to fincas; 82° 45' W, 8° 55' N, 1600 m; montane rain forest zone, disturbed primary forest, on bark (lower stem), fully shaded; Jun 2002, *Lücking 15106* (INB).

***Thelotrema hypoprotocetraricum* (Hale) Hale** (Fig. 32A)

Thelotrema hypoprotocetraricum (Hale) Hale, Mycotaxon 11: 131 (1980); *Leptotrema hypoprotocetraricum* Hale, Smithson. Contr. Bot. 38: 52 (1978). Holotype. Panama, *Mori & Gentry 4513* (US!).

Thallus light yellowish grey, smooth to uneven, with dense, paraplectenchymatous cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia prominent, angular-rounded, 0.8–1.5 mm diam.; disc partially covered by 0.3–0.6 mm wide pore, grey-brown, white-pruinose; proper margin entire, pale brown, undulate to fissured, thalline margin entire, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present, distinct. Paraphyses unbranched. Ascospores single, 150–250 × 30–35 µm, oblong, richly muriform, with slightly thickened septa and rectangular lumina, brown, I+ violet-blue (amyloid), at least when younger. Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids.

Remarks:—This species is unique in the genus in combining large, muriform, brown ascospores with a hypoprotocetraric chemistry. *Thelotrema occlusum* differs chiefly in the colorless ascospores.

Specimens examined:—Not yet found in Costa Rica but reported from Panama by Hale (1978).

***Thelotrema lacteum* Kremp.** (Fig. 32B)

Thelotrema lacteum Kremp. in Nylander, Flora 47: 269 (1864); *Phaeotrema lacteum* (Kremp.) Müll. Arg., Flora 70: 399 (1887). Lectotype (Hale 1981: 256). Australia, s.col. (M!; isolectotype: H-NYL 22814!).
Phaeotrema consimile Müll. Arg., Flora 70: 398 (1887). Holotype. Australia, *Sayer s.n.* (G!).
Thelotrema sitianum Vain., Étud. Class. Lich. Brésil 2: 81 (1890); *Phaeotrema sitianum* (Vain.) Zahlbr. in Engler & Prantl, Nat. Pflanzenfam. 1(1): 119 (1905); *Thelotrema lepadodes* subsp. *sitianum* (Vain.) G. Salisb., Lichenologist 5: 270 (1972). Lectotype (Salisbury, 1972: 270). Brazil, *Vainio s.n.* (TUR-VAIN 26808!; Vainio, Lich. Bras. Exs. 565).
Ocellularia cricota F. Wilson in Bailey, Bot. Bull. Dept Agric., Queensland 7: 32 (1891); *Phaeotrema cricotum* (F. Wilson) Müll. Arg., Hedwigia 32: 130 (1893). Lectotype (Hale 1981: 256). Australia, *Wilson s.n.* (G!; isolectotype: BRI!).
Ocellularia zeorina Müll. Arg., Nuovo Giorn. Bot. Ital. 23: 394 (1891). Holotype. Australia, *Bailey 460* p.p. (G!).
Ocellularia annulosa Müll. Arg., Bull. Herb. Boissier 3: 314 (1895). Holotype. Australia, *Shirley s.n.* (G!; isotype: BRI!).
Ocellularia japonica Zahlbr., Ann. Mycol. 14: 49 (1916). Lectotype (Hale 1981: 256). Japan, *Tsunoda s.n.* (W!).

Thallus white to light yellowish grey, smooth to uneven, with loose cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.5–0.9 mm diam.; disc partially covered by 0.3–0.6 mm wide pore, brown-black, white-pruinose; proper margin entire, dark brown, undulate to fissured, thalline margin entire, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, pale brown; periphysoids present, distinct. Paraphyses unbranched, thick. Ascospores 2–8/ascus, 60–150 × 8–12 µm, fusiform with distal ends tapering, 17–27-septate, with thick septa and lens-shaped lumina, pale grey-brown, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This species is similar to *Thelotrema pachysporum* (see below) and has been much confused with the latter in the literature. Both species agree in the whitish thallus and brown, transversely septate ascospores. However, the ascospores are distinctly smaller in *T. pachysporum* and that species lacks a thallus cortex. These differences are reflected in the molecular phylogeny, where *T. pachysporum* clusters within the *T. monosporum* complex whereas *T. lacteum* falls within the *T. lepadinum* complex (Lumbsch *et al.* 2008; Rivas Plata *et al.* 2010a).

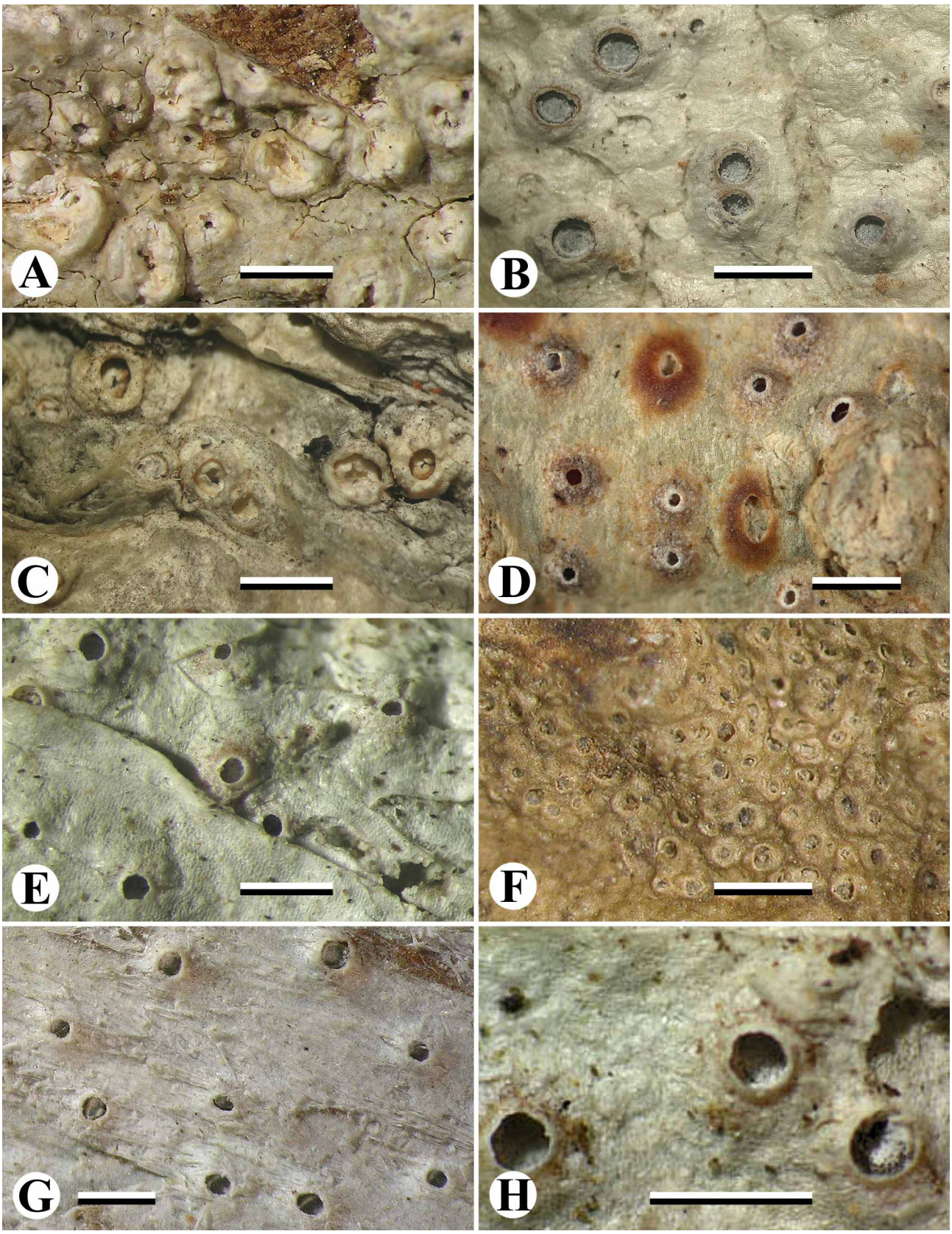

FIGURE 32. A. *Thelotrema hypoprotocetraricum*. B. *Thelotrema lacteum*. C. *Thelotrema lepadinum*. D. *Thelotrema lepadodes*. E. *Thelotrema monosporum*. F. *Thelotrema myriocarpum*. G–H. *Thelotrema pachysporum*. Scale = 1 mm.

Specimens examined:—COSTA RICA. Alajuela: Maquenque Mixed National Wildlife Refuge, Huetar Norte; 84° 11' W, 10° 42' N, 0–100 m; Apr 2005, *Chaves 2302* (INB). Volcán Tenorio National Park, Pilón Biological Station (Arenal-Tempisque Conservation Area), Tilarán Ridge, 140 km NW of San José, 25 km NNW of Tilarán, near Bijagua, access road to station and river; 84° 59' W, 10° 43' N, 700 m; lower montane cloud forest zone, exposed trees and fence posts along pasture, on bark (lower trunk), exposed; Mar 2004, *Sipman 51802* (B, INB). Guanacaste: Monte Alto Forest Reserve, Monte Alto Biological Station (Tempisque Conservation Area), Nicoya Pensinsula, 150 km W of San José, 10 km SSE of Nicoya, near Hojancha, main trails and access road through reserve near station (Sendero Jardín de Orquideas, Sendero Ceiba, Sendero Shannon-Ward); 85° 24' W, 10° 02' N, 450–550 m; lowland to lower montane moist forest zone, disturbed primary and oldgrowth secondary forest, on bark (lower trunk) of *Croton draco*, exposed; Mar 2004, *Sipman 51959* (B, INB). San José: Along road from San Jerónimo to Alto La Palma, N of San José; 10° 00' N, 84° 01' W, 1500 m; on fence poles and scattered trees among pasture fields and gardens; Nov 1988, *Sipman et al. 41543* (B, CR). Also reported as *Phaeotrema consimile* from Costa Rica (Müller Argoviensis, 1893) but we have not checked that record and it might represent either this species or *Thelotrema pachysporum*.

***Thelotrema lepadinum* (Ach.) Ach.** (Fig. 32C)

Thelotrema lepadinum (Ach.) Ach., Method. Lich.: 132 (1803); *Lichen lepadinus* Ach., Lichenograph. Suec. Prodr.: 30 (1798). Lectotype (Purvis *et al.*, 1995: 344). Sweden, *Acharius s.n.* (UPS-ACH!).

Volvaria truncigena DC in Lamarck & De Candolle, Flor. France 3(2): 374 (1805). Type. France, *Dufour s.n.* (PC, not seen).

Lichen inclusus Sowerby, Col. Fig. Engl. Fung. Mushr. 3 (1800); *Thelotrema inclusum* (Sowerby) Funck, Cryptog. Gewächse 2: 4 (1808). Holotype: England, s.col. (not seen).

Thelotrema aemulans Kremp., Verh. Zool.-Bot. Ges. Wien 26: 453 (1876); *Leptotrema aemulans* (Kremp.) Müll. Arg., Bull. Herb. Boissier 2, App. 1: 75 (1893). Holotype. New Zealand, *Knight s.n.* (M!).

Thelotrema flavescens Darb. in Nordenskjöld, Wiss. Ergebn. Schwed. Südpolarexped. 1901–1903, 4(4): 6 (1912). Holotype. Chile, *Skottsberg s.n.* (S!).

Thelotrema periphysatum Zahlbr., Denkschr. Math.-Nat. Kl. K. Akad. Wiss. Wien 104: 264 (1941). Holotype. New Zealand, *Allan 102* (W!).

Thelotrema obconicum Räsänen, Suom. Elain-ja Kasvit. Seuran Van. Tiedon. Pöytäkirjat 3: 184 (1949). Holotype. Australia, *Wilson s.n.* (H!).

Thelotrema osornense C. W. Dodge, Nova Hedwigia 12: 331 (1966). Holotype. Chile, *Dodge & Dodge 28* (FH!).

Thallus light greyish yellow to greyish olive, smooth to uneven, with irregular, compacted cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia prominent to sessile, rounded, 0.5–1.8 mm diam.; disc partially covered by 0.3–1 mm wide pore, brown, white-pruinose; proper margin entire, pale brown, undulate, thalline margin entire, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present, distinct. Paraphyses unbranched. Ascospores 1–4/ascus, 65–120 × 16–26 µm, ellipsoid, richly muriform, with thick septa and rounded lumina, thick-walled, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Thelotrema lepadinum* is the most widespread species in the entire family Graphidaceae, with a nearly cosmopolitan distribution. Molecular data from collections representing a wide geographic range support monophyly of this taxon (Lumbsch *et al.* 2008). The species is characterized by comparatively large, prominent to sessile apothecia, in combination with muriform, thick-walled, amyloid ascospores. It can hardly be confused with any other species in the genus; the superficially similar T. weberi Hale has narrower, always sessile apothecia with a narrow pore and contains norstictic acid.

Specimens examined:—COSTA RICA. Cartago: Cordillera de Talamanca, 3.5 km S of El Empalme, Interamerican Highway; 9° 41' N, 83° 55' W, 2500 m; montane rain forest zone, on trunks of scattered moribund trees in pasture; Dec 1978, *Sipman 11609* (U). Cartago: Tapantí National Park, Macizo de la Muerte Section, Cerro de la Muerte (La Amistad Pacífico Conservation Area), Talamanca Ridge, Villa Millskm 95 on

road (ruta 2) from Cartago to San Isidro, trail behind Restaurante La Georgina (Sendero La Danta); 83° 43' W, 9° 33' N, 3100 m; upper montane rain forest zone, disturbed oak forest, on bark (lower trunk), semi-exposed; Apr 2003, *Buck 44257* (INB, NY). Heredia: Volcán Barba, N of Heredia, along track Sacramento to entrance Braulio Carillo National Park; 10° 08' N, 84° 05' W, 2550 m; pastureland with relict trees of *Quercus* forest; Mar 1985, *Sipman 20591* (B, CR). San José: Cordillera de Talamanca, Interamerican Highway near El Empalme, S side of the highway to San Pablo; 9° 13' N, 83° 37' W, 2200 m; lower mountain rainforest; Dec 1978, *Kalb & Plöbst 38927* (hb. Kalb). Los Chesperitos restaurant (La Amistad Pacífico Conservation Area), Talamanca Ridge, on road (ruta 2) from Cartago to San Isidro, roadside; 83° 49' W, 9° 37' N, 2800 m; upper montane rain forest zone, forest remnants and partially exposed trees along roadside, on bark (lower trunk), semi-exposed; Apr 2003, *Grube 11710* (GZU, INB). Along trail to triangulation station on top of Tumba Vieja; 90–200 m; Dec 1934, *Dodge et al. s.n.* [FH; as *Leptotrema postpositum* (Nyl.) Zahlbr.].

***Thelotrema lepadodes* Tuck.** (Fig. 32D)

Thelotrema lepadodes Tuck., Proc. Amer. Acad. Arts Sci. 5: 405 (1862); *Leptotrema lepadodes* (Tuck.) Zahlbr., Cat. Lich. Univ. 2: 636 (1923). Lectotype (Hale 1978: 52): Cuba, *Wright s.n.* (FH!).

Thelotrema monosporum f. *album* Nyl., Ann. Sci. Nat. Bot., Ser. 4, 15: 46 (1861); *Leptotrema monosporum* f. *album* (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 638 (1923). Holotype: Japan, *Wright s.n.* (FH!).

Thelotrema monosporum var. *patulum* Nyl., Acta Soc. Sci. Fenn. 7: 452 (1863); *Leptotrema patulum* (Nyl.) Müll. Arg., Bull. Herb. Boissier 3: 315 (1895). Lectotype (Hale 1978: 52): Colombia, *Lindig s.n.* (H-NYL 22715!; isolectotype: H-NYL 22717!).

Thelotrema disciforme Leight., Trans. Linn. Soc. London 27: 170 (1869); *Phaeotrema disciforme* (Leight.) Hale, Smithsonian Contr. Bot. 16: 29 (1974). Lectotype (Frisch 2006: 300): Sri Lanka, *Thwaites 128 p.p.* (BM!; isolectotype: H-NYL 3851!).

Leptotrema aemulum Müll. Arg., Bull. Herb. Boissier 3: 316 (1895). Lectotype (Mangold *et al.* 2009: 379): Australia, *Knight 295* (G!).

Thelotrema tantali Zahlbr., Ann. Mycol. 10: 371 (1912). Holotype. U.S.A. (Hawaii), *Lyon s.n.* (W!).

Thelotrema rarotongae Räsänen ex Sbarbaro, Archiv. Bot. 15: 101 (1939). Holotype. Cook Islands, *Parks & Parks 2* (H!).

Leptotrema pinarocarpum Zahlbr. in Magnusson & Zahlbruckner, Arkiv Bot. 31A: 46 (1943). Lectotype (Hale 1978: 52): U.S.A. (Hawaii), *Faurie 679* (UPS!).

Leptotrema bisporum Szatala, Ann. Mus. Nat. Hungar., N.S., 7: 30 (1956). Holotype: Papua New Guinea, *Biró 254* (BP!).

Thallus whitish to light yellowish grey, smooth to uneven, ecorticate; photobiont layer with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.5–1 mm diam.; disc partially covered by 0.4–0.7 mm wide pore, brown-black, white-pruinose; proper margin entire, dark brown, undulate, thalline margin entire, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, pale brown; periphysoids present, distinct. Paraphyses unbranched, thick. Ascospores 2–8/ascus, 60–110 × 15–25 µm, oblong with distal ends tapering, richly muriform, with thick septa and rounded lumina, brown, young I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—This species belongs in the *Thelotrema monosporum* complex, which is characterized by ecorticate, usually whitish thalli and brown ascospores. The species has been much confused with *T. monosporum* (see below) until molecular phylogeny clarified the species concept (Lumbsch *et al.* 2008; Lücking 2009; Mangold *et al.* 2009; Rivas Plata *et al.* 2010a). Thus, *T. lepadodes* and *T. monosporum* differ in ascospore type: comparatively thick-walled and with thickened septa and remaining colorless and amyloid for a long time in *T. lepadodes* versus thin-walled with thin septa and soon becoming brown and non-amyloid in *T. monosporum*. Except for the longitudinal septa, the ascospores of *T. lepadodes* are therefore similar to those of *T. pachysporum* (see below).

Specimens examined:—COSTA RICA. Limón: Gandoca-Manzanillo Wildlife Refuge, Manzanillo Section (La Amistad Caribe Conservation Area), Manzanillo, 170 km ESE of San José, 65 km SE of Limón,

trail along beach; 82° 53' W, 9° 38' N, sea level; lowland coastal moist forest zone, disturbed coastal vegetation with *Cocos nucifera*, *Coccoloba uvifera*, and *Rhizophora mangle*, on wood of *Terminalia*, partially exposed; Mar 2004, *Aptroot 60324* (BR, INB). Puntarenas: Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, beach south of station; 83° 36' W, 8° 28' N, sea level; lowland coastal rain forest zone, disturbed coastal forest and exposed trees along beach, on bark (lower stem), exposed; Apr 2003, *Sipman 51135b* (B, INB). Puntarenas: Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), fully shaded; Feb 1997, *Lücking 97-128* (F).

***Thelotrema monosporum* Nyl.** (Fig. 32E)

Thelotrema monosporum Nyl., Ann. Sci. Nat., Bot., Ser. 4, 15: 46 (1860). Lectotype (Hale 1981: 260). New Caledonia, *Pancher s.n.* (H-NYL 22709!).

Thallus whitish to light yellowish grey, smooth to uneven, ecorticate; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.5–1 mm diam.; disc covered by narrow, 0.1–0.3 mm wide pore, barely visible; proper margin entire, dark brown, white-pruinose, undulate, thalline margin entire, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, pale brown; periphysoids present, distinct. Paraphyses unbranched, thick. Ascospores 1–4/ascus, 40–100 × 15–30 µm, oblong to fusiform, richly muriform, with thin to slightly thickened septa and rectangular lumina, brown, I– (non-amyloid), richly muriform. Secondary chemistry: no substances detected by TLC.

Remarks:—The concept of *Thelotrema monosporum* has been very confused in the literature, mostly referring to specimens with muriform, brown ascospores and lacking secondary substances. Revision of type material and molecular phylogeny show that at least five distinct species are involved in this complex, two resembling *T. lepadinum* with corticate thalli, *T. saxatile* C. Knight and *T. lepademersum* Nagarkar, Sethy & Patw., and three with ecorticate, whitish thalli, *T. lepadodes*, *T. monosporum*, and *T. monosporoides* Nyl. (Rivas Plata *et al*. 2010a). *Thelotrema monosporum* thus combines a whitish, ecorticate thallus with muriform, brown, non-amyloid ascospores with rather thin septa about 60–120 µm long. Its closest relative is *T. monosporoides* which differs only in the longer ascospores (120–200 µm).

Specimens examined:—COSTA RICA. Puntarenas: La Amistad International Park, Altamira Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 20 km N of San Vito near Finca Colorado, trail to Casa Coca; 83° 00' W, 9° 02' N, 1600–1800 m; montane rain forest zone, secondary forest and open secondary vegetation dominated by *Cecropia*, on bark (lower trunk), semi-exposed; Jul 2002, *Sipman 48042e* (B, INB).

***Thelotrema myriocarpum* Fée** (Fig. 32F)

Thelotrema myriocarpum Fée, Essai sur les Cryptogames des Écorces Exotiques Officinales (Paris) 1: 94 (1824); *Myriotrema myriocarpum* (Fée) Hale, Mycotaxon 11: 134 (1980). Lectotype (Hale 1978: 45). South America, s.col. (PC!; isolectotypes: H!, L!).

Thallus light yellow-olive, smooth to uneven, with dense, paraplectenchymatous cortex; photobiont layer with scattered clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.25–0.35 mm diam.; disc partially covered by 0.15–0.25 mm wide pore, pale brown, thinly white-pruinose; proper margin fissured, pale brown, fissured, thalline margin entire, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present, indistinct. Paraphyses unbranched. Ascospores 8/

ascus, muriform, ellipsoid with distal end tapering, 20–40 × 7–10 µm, with slightly thickened septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: stictic, constictic, α-acetylconstictic, cryptostictic, α-acetylhypoconstictic, and hypostictic acids.

Remarks:—This species was included in *Myriotrema* (Hale 1980) but on account of the (indistinct) periphysoids and stictic acid chemistry is better placed in *Thelotrema* (Mangold *et al.* 2009). There are several similar species with dense cortex, small, muriform ascospores, and stictic acid, none occurring in Central America: *T. crassisporum* Mangold has larger, prominent apothecia and much smaller but broad ascospores; *T. cupulare* Müll. Arg. has very large apothecia resembling those of *Chapsa platycarpa*; and *T. zimbabwense* Frisch differs by its conspicuously folded thallus and narrow-pored apothecia.

Thelotrema occlusum Nyl.

Thelotrema occlusum Nyl., Ann. Sci. Nat., Bot., Ser. 5, 7: 318 (1867). Lectotype (Hale 1978: 47). Colombia, *Lindig s.n.* (H-NYL 22522!).

Thallus light yellowish grey, verrucose, smooth to uneven, with loose cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent, angular-rounded, 0.6–1 mm diam.; disc partially covered by 0.2–0.4 mm wide pore, grey-brown, white-pruinose; proper margin entire, pale brown, undulate to fissured, thalline margin entire, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present. Paraphyses unbranched. Ascospores single, 100–220 × 15–40 µm, oblong, richly muriform, with slightly thickened septa and rectangular lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids.

Remarks:—This species is very similar to *Thelotrema hypoprotocetraricum* and chiefly differs in the persistently colorless ascospores. *Thelotrema conveniens* agrees general morphology and ascospore type but lacks secondary substances.

Specimens examined:—This species is not yet known from Costa Rica but was reported from Panama (Hale 1978).

Thelotrema pachysporum **Nyl.** (Fig. 32G–H)

Thelotrema pachysporum Nyl., Bull. Soc. Linn. Normandie, Sér. 2, 2: 72 (1868). Lectotype (Frisch, 2006: 306). New Caledonia, *Pancher s.n.* (H-NYL 22747!).

Thelotrema cavatum var. *dolichosporum* Nyl., Ann. Sci. Nat. Bot., Ser. 4., 11: 242 (1859); *Thelotrema dolichosporum* (Nyl.) Nyl., Bull. Soc. Linn. Normandie, Sér. 2, 2: 72 (1868); *Ocellularia dolichospora* (Nyl.) Müller Arg., Mém. Soc. Phys. Hist. Nat. Genève 29(8): 9 (1887). Polynesia, *Mercier s.n.* (PC!).

Thelotrema exalbidum Stirt., Proc. Roy. Philos. Soc. Glasgow 13: 184 (1881); *Leptotrema exalbidum* (Stirt.) Zahlbr., Cat. Lich. Univ. 2: 634 (1923). Lectotype (Hale 1974: 29): India, *Watt s.n.* (BM!; isolectotype: GLAM!).

Thelotrema galactinum Vain., Dansk Bot. Ark. 4, 11: 24 (1926); *Phaeotrema galactinum* (Vain.) Zahlbr., Cat. Lich. Univ. 8: 245 (1932). Lectotype: Mexico, *Liebmann 7712* (C!).

Thelotrema limae Vain., Bol. Soc. Brot., Sér. 2, 6: 150 (1929); *Phaeotrema limae* (Vain.) Zahlbr., Cat. Lich. Univ. 10: 216 (1939). Holotype: Mozambique, *Pires de Lima 38* (TUR-VAIN 34808!).

Thelotrema palmense Vain., Bol. Soc. Brot., Sér. 2, 6: 150 (1929); *Phaeotrema palmense* (Vain.) Zahlbr., Cat. Lich. Univ. 10: 216 (1939). Lectotype (Salisbury, 1972: 270): Mozambique, *Pires de Lima 78* (TUR-VAIN 34810!).

Thallus whitish to light yellowish grey, smooth to uneven, ecorticate; photobiont layer with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.4–1.3 mm diam.; disc partially covered by 0.2–0.6 mm wide pore, brown-black, white-pruinose; proper margin entire, dark brown, undulate, thalline margin entire, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, pale brown; periphysoids present, distinct. Paraphyses unbranched, thick. Ascospores 8/ascus, 35–75 × 9–13 µm,

fusiform with distal ends tapering, 7–15-septate, with thick septa and rounded lumina, thick-walled, brown, young I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Thelotrema pachysporum* is often confused with *T. lacteum* (see above), which also has a whitish thallus and brown, transversely septate ascospores. However, the latter has a loose thallus cortex and the ascospores are much longer, often over 100 µm. *Thelotrema pachysporum* is closely related to *T. lepadodes* (see above), which agrees in all features except that the ascospores are muriform.

Specimens examined:—COSTA RICA. Puntarenas: Carara National Park, Quebrada Bonita Section (Pacífico Central Conservation Area), 60 km WSW of San Jose on road from Orotina to Quepos (34), trail from visitor's center to Quebrada Bonita; 84° 35' W, 9° 47' N, 100 m; lowland moist forest zone, partly disturbed dense primary forest with understory dominated by *Erythrochiton gymnanthus*, on bark (lower stem), semi-exposed; Jul 2002, *Sipman 48392j* (B). San Vito de Coto Brus, Las Cruces Biological Station; 8° 47' N, 82° 58' W, 1200 m; about 500 m from station on road to San Vito; trunklets (Leguminosae) of living fence between meadow and gravel road; Oct 2004, *Sipman 53333* (B, INB).

Thelotrema porinoides **Mont. & Bosch** (Fig. 33A)

Thelotrema porinoides Mont. & Bosch in Junghuhn, Pl. Junghuhn. 4: 484 (1855); *Thelotrema cavatum* var. *porinoides* (Mont. & Bosch) Nyl., Mém. Soc. Sci. Nat. Cherbourg 5: 118 (1858); *Ocellularia porinoides* (Mont. & Bosch) Zahlbr., Cat. Lich. Univ. 2: 599 (1923). Lectotype (Hale 1974: 20): Indonesia (Java), *Junghuhn s.n.* (L!; isolectotypes: FH!, G!, H-NYL 22732!, PC!).

Thelotrema exanthismocarpum Leight., Trans. Linn. Soc. London 27: 169 (1869); *Ocellularia exanthismocarpa* (Leight.) Zahlbr., Cat. Lich. Univ. 2: 590 (1923). Lectotype (Hale 1974: 29): Sri Lanka, *Thwaites 97* (BM!).

Thelotrema albidiforme Leight., Trans. Linn. Soc. London 27: 170 (1869); *Ocellularia albidiformis* (Leight.) Zahlbr., Ann. Mycol. 14: 50 (1916). Holotype: Sri Lanka, *Thwaites 19* (BM!).

Thelotrema obovatum Stirt., Trans. Glasgow Soc. Field Nat. 1: 21 (1873); *Ocellularia obovata* (Stirt.) Müll. Arg., Bull. Herb. Boissier 2, App. 1: 74 (1893). Lectotype (Galloway 1985: 576): New Zealand, *Buchanan 57b* (GLAM!; isolectotype: BM!).

Ocellularia platychlamys Müll. Arg., Bull. Herb. Boissier 3: 313 (1895). Lectotype (Mangold *et al.*, 2009: 658): Australia, *Bailey s.n.* (G!).

Ocellularia multilocularis Zahlbr., Ann. Mycol. 10: 369 (1912). Holotype: U.S.A. (Hawaii), *Rock 117* (W!).

Thelotrema isertii Vain., Ann. Acad. Sci. Fenn. A 6(7): 140 (1915); *Ocellularia isertii* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 593 (1923). Lectotype (Hale 1974: 20): Lesser Antilles (Guadeloupe), *Isert 87* (C!; isolectotype: TUR-VAIN 26871!).

Thelotrema homothecium Vain., Ann. Acad. Sci. Fenn., Ser. A, 15(6): 190 (1921); *Ocellularia homothecia* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 593 (1923). Lectotype (Hale 1974: 20): Philippines, *Elmer 14852* p.p. (TUR-VAIN!; isotype: US!).

Ocellularia floridensis Fink in Hedrick, Mycologia 25: 314 (1934). U.S.A., *Fink 13094* (MICH!).

Ocellularia agasthiensis Nagarkar, Sethy & Patw. in Nagarkar *et al.*, Biovigyanam 14: 28 (1988). India, Sethy & Nagarkar 83.188b (AMH, not seen; isotype: US!).

Thallus light yellowish grey, smooth to uneven, with irregular, compacted cortex; photobiont layer with clusters of calcium oxalate crystals. Apothecia prominent, rounded, 0.5–1 mm diam.; disc partially covered by 0.3–0.6 mm wide pore, pale brown, white-pruinose; proper margin entire, pale brown, undulate, thalline margin entire, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, colorless; periphysoids present, distinct. Paraphyses unbranched. Ascospores 8/ascus, 65–140 × 12–17 µm, oblong, with thick septa and rounded lumina, thick-walled, colorless, I+ violet-blue (amyloid), 17–27-septate. Secondary chemistry: stictic, constictic and hypostictic acids.

Remarks:—*Thelotrema porinoides* is very similar to *T. diplotrema* (see above) and differs chiefly in the presence of stictic acid and the more prominent apothecia. It is one of the most common and widespread species of the genus.

Specimens examined:—COSTA RICA. Alajuela: Volcán Tenorio National Park, Pilón Biological Station (Arenal-Tempisque Conservation Area), Tilarán Ridge, 140 km NW of San José, 25 km NNW of Tilarán, near

Bijagua, access road to station and river; 84° 59' W, 10° 43' N, 700 m; lower montane cloud forest zone, exposed trees and fence posts along pasture, on bark (lower trunk), exposed; Mar 2004, *Sipman 51838* (B, INB); ibid., on bark (lower stem), partially shaded; Mar 2004, *Trest 1535a* (INB); ibid., on bark (lower trunk), fully exposed; Mar 2004, *Trest 1558a* (INB); ibid., main trail through forest to crater; 84° 59' W, 10° 43' N, 700–900 m; lower montane cloud forest zone, partly disturbed primary forest, on bark (branch, fallen), semi-exposed; Mar 2004, *Will-Wolf 12746a* (INB, WIS); ibid., on bark (lower trunk), partially shaded; Mar 2004, *Lücking 17263b* (F, INB). Cartago: Tapantí National Park, Tapantí Section, Tapantí Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 35 km SE of San José and 18 km SE of Cartago, first trail to river (Sendero La Oropéndula); 83° 47' W, 9° 45' N, 1300–1400 m; montane rain forest zone, closed primary forest and roadside, on bark (lower stem), exposed; Apr 2003, *Will-Wolf 12538i* (INB, WIS). Guanacaste: Volcán Tenorio National Park, Alto Masis Section (Arenal-Tilarán Conservation Area), Tilarán Ridge, 125 km NW of San José, 15 km NNW of Tilarán, near Tierras Morenas, surroundings of station; 85° 00' W, 10° 37' N, 950–1000 m; lower montane elfin cloud forest zone, disturbed low elfin forest and secondary vegetation, on bark (lower stem), partially shaded; Mar 2004, *Lücking 17323c* (F, INB). Puntarenas: Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), fully shaded; Feb 1997, *Lücking 97-179* (F).

Thelotrema submyriocarpum* Lücking, *spec. nov. (Fig. 33B–D)
MycoBank #800102

Differing from *Thelotrema myriocarpum* in the smaller ascospores.

Holotype:—COSTA RICA. Puntarenas: Vicinity of Monteverde near Hotel de la Montaña; 1400 m; on scattered trees in pastures; Jan 1979, *Egan 11713* (MIN).

Thallus light yellow-white, coarsely uneven, rather thick, with dense, paraplectenchymatous cortex; photobiont layer and medulla with abundant clusters of calcium oxalate crystals. Apothecia immersed, rounded to shortly elongate, 0.3–0.5 mm diam.; disc partially covered by 0.2–0.35 mm wide pore, pale brown, thinly white-pruinose; proper margin entire, pale brown, white-pruinose, thalline margin entire, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, grey-brown; periphysoids present. Hymenium 100–120 µm high; paraphyses unbranched; asci 80–100 × 10–15 µm. Ascospores 8/ascus, submuriform with 3–5 transverse septa and 0–2 longitudinal septa per segment, ellipsoid, 15–20 × 8–12 µm, with thin septa and rectangular lumina, colorless, I– (non-amyloid). Secondary chemistry: stictic, constictic, cryptostictic, and hypostictic acids.

Remarks:—This new species agrees in most aspects with *Thelotrema myriocarpum* (see above), except for the smaller ascospores. Also similar is *T. leucophthalmum* Nyl., which has larger, erumpent to prominent apothecia and larger ascospores. The new species should not be confused with *Leucodecton subcompunctum* (see above), which looks very similar superficially but has smaller apothecia, lacks periphysoids, and has brown ascospores.

***Thelotrema subtile* Tuck.** (Fig. 33E, 35D–E)

Thelotrema subtile Tuck., Amer. J. Arts and Sci., Ser. 2, 25: 426 (1858); *Ocellularia subtilis* (Tuck.) Riddle, Mycologia 15: 79 (1923). Lectotype (Salisbury 1972: 263; Mangold *et al.* 2009: 658): U.S.A, *Frost 150* p.p. (FH!; isolectotype: NY!, Tuckerman, Reliquiae Tuckermanianae 140).

Ocellularia bonplandii var. *obliterata* Müll. Arg., Bull. Herb. Boissier 1: 54 (1893). Holotype: Australia, *Wilson 513* (G!; isotype: NSW!).

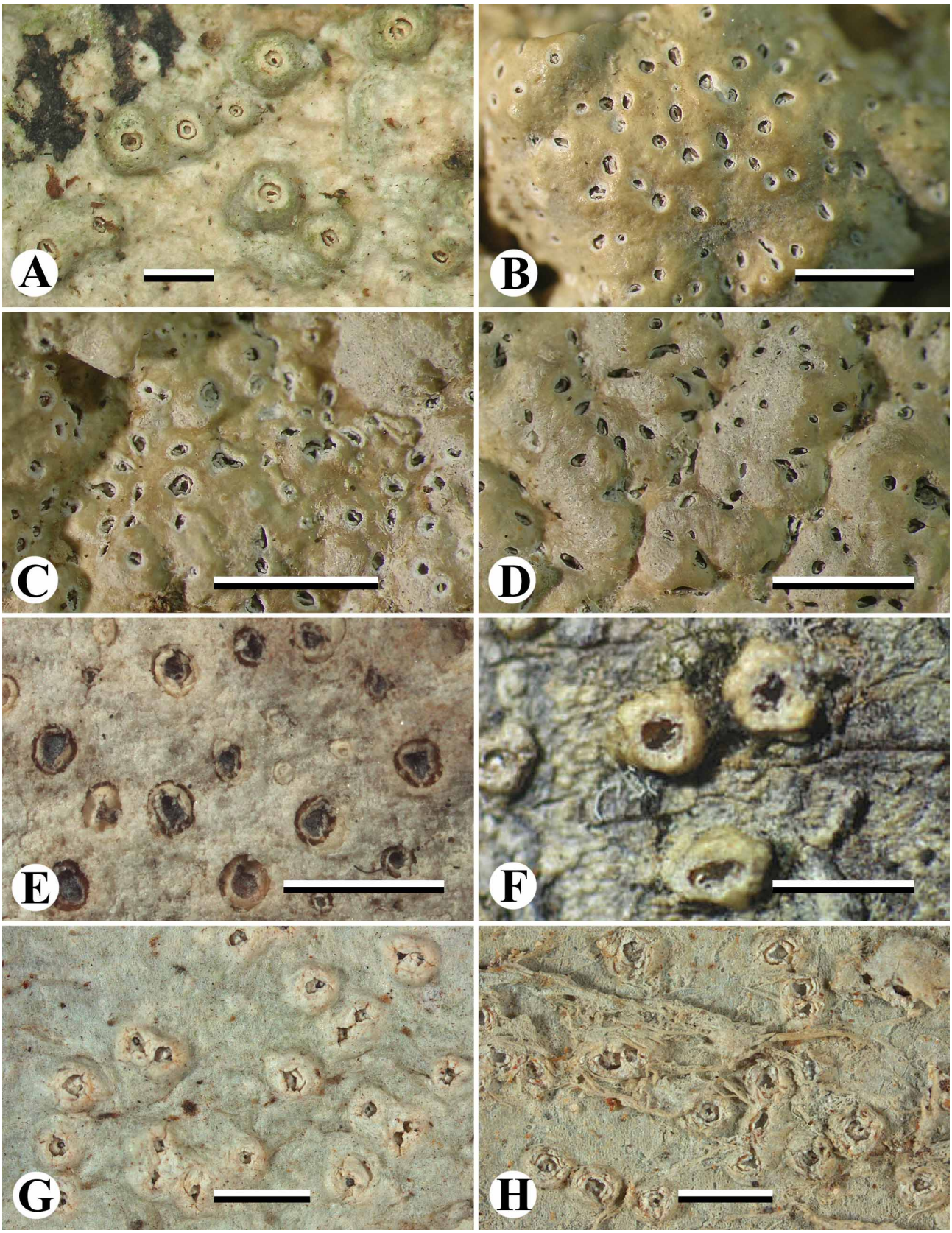

FIGURE 33. A. *Thelotrema porinoides*. B–D. *Thelotrema submyriocarpum*. E. *Thelotrema subtile*. F. *Thelotrema suecicum*. G–H. *Thelotrema wilsonii*. Scale = 1 mm.

Thallus whitish to light yellowish grey, smooth to uneven, ecorticate and usually poorly developed and in part endoperidermal; photobiont layer with clusters of calcium oxalate crystals. Apothecia immersed (to erumpent), rounded, 0.3–0.5 mm diam.; disc partially covered by 0.2–0.3 mm wide pore, brown-black, thinly white-pruinose (usually appearing dark); proper margin undulate, pale brown; thalline margin entire, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, colorless to pale yellowish brown; periphysoids present, distinct. Paraphyses unbranched. Ascospores 4–8/ascus, 25–45 × 6–10 µm, oblong with distal ends tapering, 7–15-septate, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Thelotrema subtile* forms part of a complex of species with small, transversely septate, usually colorless ascospores and lacking secondary substances. The two most common and widespread species, *T. subtile* and *T. suecicum* (see below), are often confused or misidentified in the literature (Lumbsch *et al.* 2008; Mangold *et al.* 1009). Lumbsch *et al.* (2008) introduced a new species, *T. pseudosubtile* Mangold, for Australian material, and Lücking *et al.* (2011) reinstated *T. lathraeum* Tuck., kept as synonym of *T. subtile* by Rivas Plata *et al.* (2010a). Further revision of the type material of names belonging to this complex revealed that some of the names were still misapplied, and the correct concept and nomenclature of the species of this complex should be as follows (see also Table 3):

Thelotrema lathraeum Tuck. (Fig. 35A); thallus with dense, prosoplectenchymatous cortex; apothecia erumpent, to 0.15 mm diam.; ascospores 5–9-septate, 15–25 × 5–7 µm, with thickened septa and angular to lens-shaped lumina, colorless, I+ violet-blue (amyloid). This species is recognized by the dense thallus cortex (resembling that of *Myriotrema* or *Ocellularia*) and the very small, erumpent apothecia and small ascospores.

Thelotrema demersum (Müll. Arg.) G. Salisb. (Fig. 34C–D) [≡ *Ocellularia demersa* Müll. Arg.; ≡ *Pyrenula clandestina* Fée, nom. illeg.; ≡ *Thelotrema albidulum* Nyl., nom. nov. inval.]; thallus with irregular, loose to compacted cortex; apothecia immersed, to 0.3 mm diam.; ascospores 7–11-septate, 20–30 × 5–7 µm, with thick septa and lens-shaped lumina and thick outer wall, colorless, I+ violet-blue (amyloid).

Thelotrema defossum (Müll. Arg.) Mangold (Fig. 34A–B); thallus with irregular, loose to compacted cortex; apothecia immersed, to 0.3 mm diam.; ascospores 5–11-septate, 15–35 × 5–8 µm, with slightly thickened septa and angular to lens-shaped lumina, colorless, I+ weakly violet-blue (amyloid). *Thelotrema demersum* and *T. defossum* are very similar in external appearance, having a well-developed thallus with small, immersed apothecia. The main difference is in the ascospores, which are only weakly amyloid in *T. defossum* and lack the thick outer wall characteristic of most of the species in this complex.

TABLE 3. Comparison of species of the *Thelotrema subtile* complex, arranged by cortex type, ascomata emergence, and ascospore wall thickness.

Species	Cortex	Ascomata	Ascospores	Ascospore size	Amyloidity	Wall
lathraeum	dense	erumpent	5–9-septate	15–25 × 5–7 µm	I+ violet-blue	thin
jugale	compacted	immersed	7–15-septate	30–60 × 6–9 µm	I+ violet-blue	thin
suecicum	compacted	prominent	5–11-septate	20–40 × 8–12 µm	I+ violet-blue	thick
defossum	loose	immersed	5–11-septate	15–35 × 5–8 µm	I+ weakly violet-blue	thin
demersum	loose	immersed	7–11-septate	20–30 × 5–7 µm	I+ violet-blue	thick
subtile	absent	immersed	7–15-septate	25–45 × 6–10 µm	I+ violet-blue	thick

Thelotrema jugale* (Müll. Arg.) Lücking, *comb. nov. (Fig. 34E–H) [MycoBank #800227; *Ocellularia jugalis* Müll. Arg., Bull. Herb. Boissier 3: 313 (1895). Holotype. Australia, *Shirley 1836* (G!; isotype: BRI!); = *Thelotrema pseudosubtile* Mangold]; thallus with compacted cortex; apothecia immersed, to 0.6 mm diam.; ascospores 7–15-septate, 30–60 × 6–9 µm, with thick septa and lens-shaped lumina, colorless, I+ violet-blue (amyloid). This species is similar to *T. demersum* and *T. defossum* but differs in the more compacted, glossy thallus cortex and the larger apothecia and larger ascospores, which lack a thick outer wall. Revision of the type material of *Ocellularia jugalis* (Fig. 34E–F) showed that it agrees with the type of *T. pseudosubtile* (Fig.

34G–H) in all relevant characters and therefore is an earlier name for that species; it is different from *T. subtile* s.str. to which it was assigned as a synonym (Mangold *et al*. 2009).

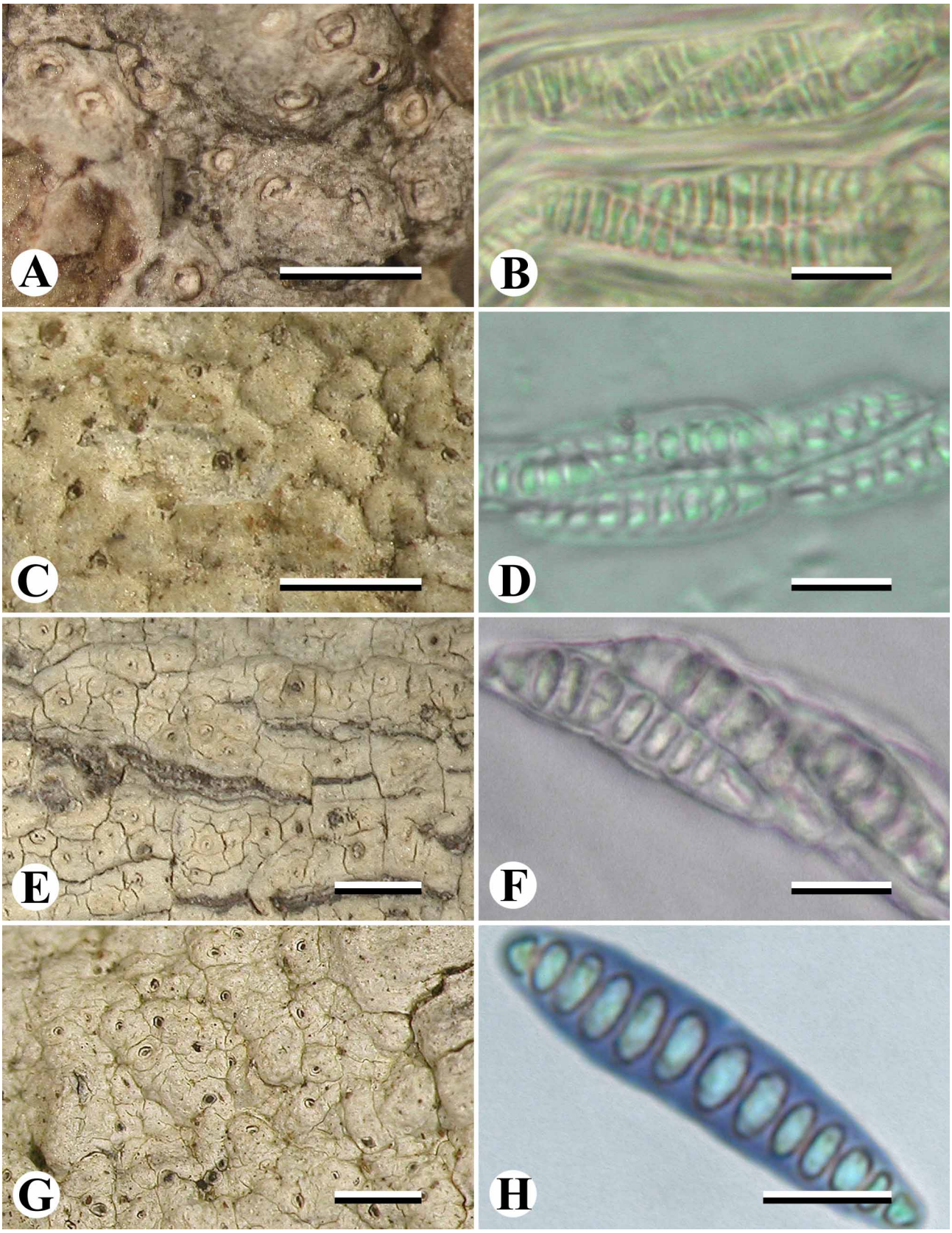

FIGURE 34. A–B. *Thelotrema defossum*. C–D. *Thelotrema demersum*. E–H. *Thelotrema jugale* (E–G, type of *Ocellularia jugalis*; G–H, type of *Thelotrema pseudosubtile*). Scale in A, C, E, G = 1 mm, in B, D, F, H = 10 µm.

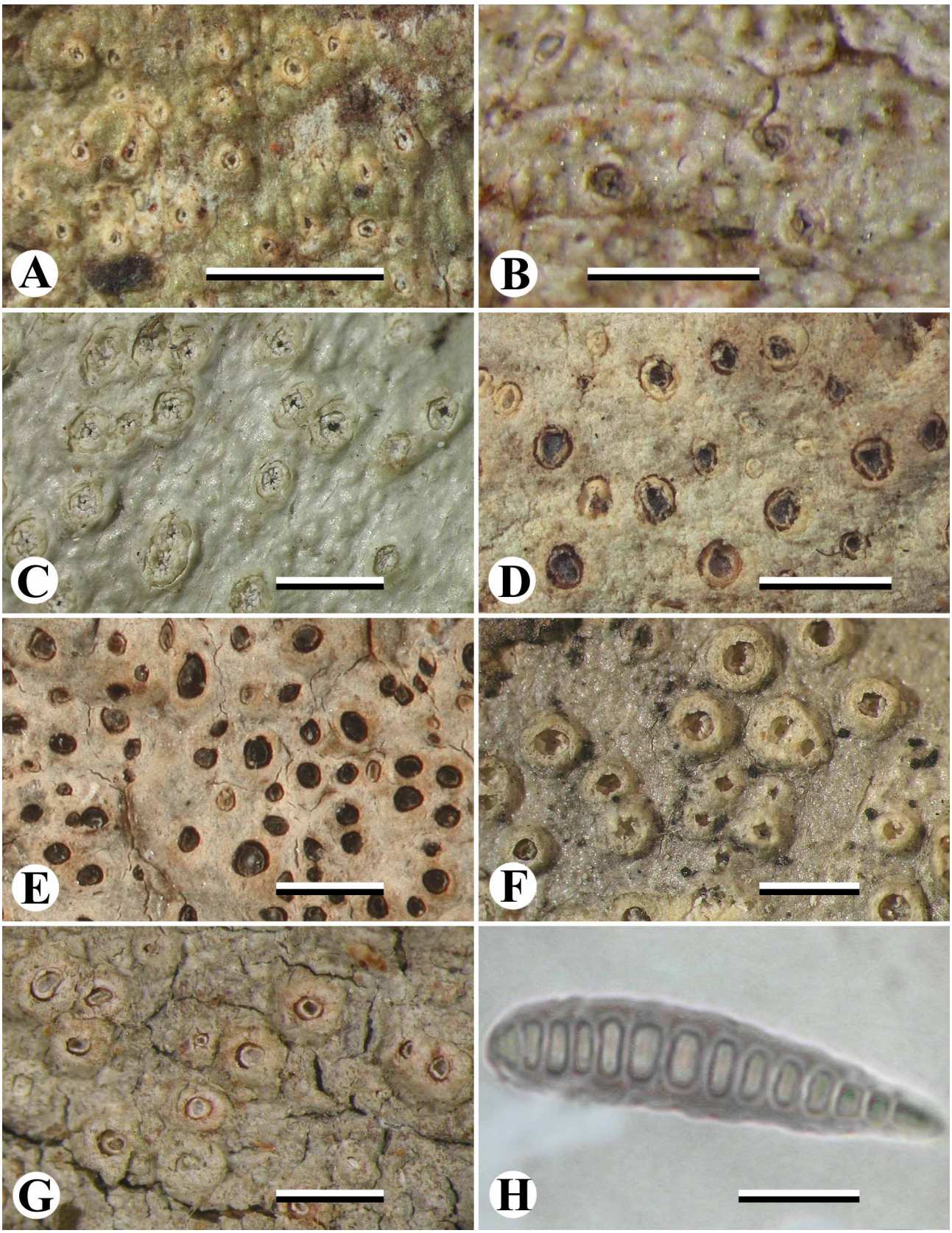

FIGURE 35. A. *Thelotrema lathraeum*. B. *Thelotrema parvizebrinum*. C. *Thelotrema petractoides*. D–E. *Thelotrema subtile* (D, type of *Thelotrema subtile*; E, type of *Ocellularia bonplandii* var. *obliterata*). F. *Thelotrema suecicum*. G–H. undescribed species of *Thelotrema* from Australia. Scale = 1 mm except H = 10 µm.

Thelotrema subtile s.str. (Fig. 33E, 35D–E) [= *Ocellularia bonplandii* var. *obliterata* Müll. Arg.]; thallus ecorticate to endoperidermal; apothecia immersed, to 0.5 mm diam., with darkened disc; ascospores 7–15-septate, 25–45 × 6–10 µm, with thick septa and lens-shaped lumina and thick outer wall, colorless, I+ violet-blue (amyloid). This species differs from the preceeding species in the poorly developed, more or less endoperidermal thallus and often darkened disc. *Ocellularia bonplandii* var. *obliterata* was given as a synonym of *T. suecicum* by Mangold *et al.* (2009) but the type agrees perfectly with the type of *T. subtile*. Lumbsch *et al.* (2008) and Mangold *et al.* (2009) mention as one of the main characters of the species the ascospore becoming brown with age. However, this is due to a misinterpretation of the available material. *Thelotrema subtile* s.str., as reported in the literature, always has colorless ascospores (James 1977; Harris 1995; Smith *et al.* 2009). Specimens with ascospores becoming brownish that were reported from Australia (Lumbsch *et al.* 2008; Mangold *et al.* 2009) are not that species but represent an undescribed taxon, differing from *T. subtile* also in the prominent apothecia and well-developed thallus (Fig. 35G–H). Coincidentally, these specimens were sequenced by Lumbsch *et al.* (2008) and fell on a clade including *T. monosporum* and related taxa, with brown ascospores, separate from the clade including the bulk of the species of the *T. subtile* complex.

Thelotrema suecicum (Fig. 33F, 35F) (see below); thallus with irregular, compacted cortex; apothecia prominent, to 0.8 mm diam.; ascospores 5–11-septate, 20–40 × 8–12 µm, with thick septa and lens-shaped lumina and thick outer wall, colorless, I+ weakly violet-blue (amyloid). This species is distinguished from all others in this group by the more or less yellowish thallus with compacted cortex and prominent apothecia; it resembles a diminutive *T. lepadinum*.

Thelotrema petractoides (Fig. 35C); thallus ecorticate, endoperidermal; apothecia prominent, to 0.8 mm diam., with concentrically layered excipulum; ascospores 7–15-septate, 25–45 6–10 µm, with thick septa and lens-shaped lumina and thick outer wall, colorless, I+ violet-blue (amyloid). This resembles a *Schizotrema* but forms part of the *Chapsa-Thelotrema* clade, although it does not cluster with either genus (Rivas Plata *et al.* 2012c).

Thelotrema parvizebrinum Mangold (Fig. 35B); thallus with irregular, compacted and shiny cortex; apothecia immersed to erumpent, to 0.2 mm diam., with concentrically layered excipulum; ascospores 3–7-septate, 12–20 × 4–7 µm, with thick septa and lens-shaped lumina and thick outer wall, colorless, I+ violet-blue (amyloid). The latter two species differ from the other species in this complex by the usually layered, apically darkened excipulum, giving them the appearance of a *Schizotrema* species. *Thelotrema petractoides* is otherwise similar to *T. suecicum* in the large, prominent apothecia, but differs in the whitish, endopermidermal thallus and apothecia with fissured thalline margin; *T. parvizebrinum* otherwise resembles *T. lathraeum* in the verruculose thallus with shiny cortex and the small apothecia and ascospores

Specimens examined:—COSTA RICA. San José: Cerro Central de Zurquí; 1600–1700 m; Dec 1929, *Dodge et al. s.n.* (FH; as *Thelotrema leucomelaenum* Nyl.).

***Thelotrema suecicum* (H. Magn.) P. James** (Fig. 33F)

Thelotrema suecicum (H. Magn.) P. James, Lichenologist 9: 186 (1977); *Ocellularia suecica* H. Magn., Bot. Notiser 1937: 125 (1937). Lectotype (James 1977: 186): Sweden, *Magnusson s.n.* (BM!; isolectotypes: C!, GZU!, F!, H!, UPS!; Magnusson, Lich. Sel. Scandin. Exs. 230).

Thallus light yellowish grey, smooth to uneven, with irregular, compacted cortex; photobiont layer and/or medulla with clusters of calcium oxalate crystals. Apothecia prominent, angular-rounded, 0.3–0.7 mm diam.; disc partially covered by 0.2–0.4 mm wide pore, brown-black, white-pruinose; proper margin entire, pale brown, undulate, thalline margin entire, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, pale brown; periphysoids present, distinct. Paraphyses unbranched. Ascospores 4–8/ascus, 20–40 × 8–12 µm, ellipsoid, 5–11-septate, with thick septa and rounded lumina, persistently thick-walled, colorless, weakly I+ violet-blue (amyloid). Secondary chemistry: no substances detected by TLC.

Remarks:—*Thelotrema suecicum* is very closely related to *T. lepadinum* and looks like a miniature version of the latter species, with small, transversely septate ascospores. It differs from *T. subtile* in the yellowish thallus with compacted cortex, the prominent apothecia, and the weakly amyloid ascospores (see discussion above).

Specimens examined:—COSTA RICA. Cartago: Tapantí National Park, Macizo de la Muerte Section, Cerro de la Muerte (La Amistad Pacífico Conservation Area), Talamanca Ridge, km 93 on road (ruta 2) from Cartago to San Isidro, roadside; 83° 45' W, 9° 34' N, 3000–3100 m; upper montane cloud forest zone, disturbed low oak forest, on bark (lower trunk), semi-exposed; Jul 2002, *Sipman 48219* (B, INB).

Thelotrema wilsonii* Sipman & Lücking, *spec. nov. (Fig. 33G–H)
MycoBank #800103

Differing from *Thelotrema subtile* in the more prominent apothecia and presence of hypoprotocetraric acid.

Holotype:—COSTA RICA. Puntarenas: Las Cruces Biological Station, San Vito de Coto Brus; 8° 47' N, 82° 58' W, 1200 m; trail to Río Java, on branches of fallen *Ficus pertusa* on fallen trunk; Oct 2004, *Sipman 53241* (INB-0003993517; isotype: B).

Thallus white to light yellowish grey, smooth to uneven, with loose, indistinct cortex and more or less endoperidermal; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent to prominent, angular-rounded, 0.5–0.8 mm diam.; disc partially covered by 0.1–0.3 mm wide pore, pale brown, thinly white-pruinose; proper margin fissured to lobulate, layered and forming concentric rings, white; thalline margin entire or becoming fissured, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, colorless to pale brown; periphysoids present, distinct. Paraphyses unbranched. Ascospores (4–)8/ascus, 5–13-septate, 25–45 × 6–10 µm, oblong, with thick septa and lens-shaped lumina and thickened outer wall, colorless, I+ violet-blue (amyloid). Secondary chemistry: hypoprotocetraric and 4-*O*-demethylnotatic acids.

Remarks:—This new species is decidated to the memory of Robert and Catherine Wilson, founders of Wilson Botanical Gardens at Las Cruces. It resembles a *Schizotrema* due to the layered excipulum, but is here placed in *Thelotrema* because of the non-carbonized excipulum and strongly amyloid ascospores. It is most similar to *T. petractoides* P. M. Jørg. & Brodo except for the chemistry. *Thelotrema subtile* has a similar thallus and ascospores but immersed apothecia, a non-layered excipulum, and lacks secondary substances. Only two other species in *Thelotrema* are known with hypoprotocetraric acid: *T. hypoprotocetraricum* (Hale) Hale and *T. occlusum* Nyl. Both have large, muriform ascospores (Rivas Plata *et al.* 2010a). The new species should not be confused with *Chapsa referta* (see above), which agrees in the layered, non-carbonized apothecial margin but has an olive-green thallus with dense cortex.

Additional specimens examined (paratypes):—COSTA RICA. Puntarenas: Las Cruces Biological Station, San Vito de Coto Brus; 8° 47' N, 82° 58' W, 1200 m; trail young planted trees in meadow on hilltop; Oct 2004, *Sipman 53359a* (B); ibid., on thin trunk of *Terminalia amazonica*; Oct 2004, *Sipman 53305* (B, INB); ibid., on trunk of *Guazuma ulmifolia* at margin; Oct 2004, *Sipman 53364* (B, INB); ibid., on thin trunk of *Tabebouia chrysantha*; Oct 2004, *Sipman 53399* (B, INB). Las Cruces Botanical Garden, 5 km S of San Vito; 82° 57' W, 8° 43' N, 1300 m; cultivated tropical hardwoods, on bark; Jan 1979, *Nash 41600* (ASU). Surroundings of Las Cruces Tropical Botanical Garden, 4 km SSE of San Vito; 8° 43' N, 82° 58' W, 1500 m; in a premontane rainforest; Jan 1979, *Kalb & Plöbst 38943, 38924* (hb. Kalb). Fila Cruces Ridge, surroundings of Las Cruces Tropical Botanical Garden, 4 km SSE of San Vito; 8° 43' N, 82° 58' W, 1550 m; in a premontane rainforest at a waterfall; Jan 1979, *Kalb & Plöbst 31822, 38924* (hb. Kalb). Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), fully shaded; Feb 1997, *Lücking 97-117* (F).

Wirthiotrema Rivas Plata, Kalb, Frisch & Lumbsch

Wirthiotrema Rivas Plata, Kalb, Frisch & Lumbsch in Rivas Plata *et al.*, Lichenologist 42: 198 (2010). Type: *Wirthiotrema glaucopallens* (Nyl.) Rivas Plata & Kalb.

Thallus usually light grey-olive to yellowish olive, smooth to uneven, with dense, prosoplectenchymatous cortex; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed to erumpent, rounded to angular-rounded; disc covered by more or less narrow pore; margin usually entire, fused or rarely free, laterally covered by thalline layer. Columella absent. Excipulum paraplectenchymatous, pale to dark brown; periphysoids absent. Hymenium clear or inspersed. Paraphyses unbranched. Ascospores muriform, small, ellipsoid with usually rounded ends, with slightly thickened septa and angular lumina, colorless or brown, I– (non-amyloid). Secondary chemistry: stictic acid and satellite substances in most species.

Remarks:—*Wirthiotrema* was established as a new genus for the *Thelotrema glaucopallens* group (Rivas Plata *et al.* 2010b), already recognized as distinct taxonomic entity by Frisch (2006). The species of this genus resemble species of *Myriotrema* s.str., but differ in the paraplectenchymatous excipulum and the stictic acid chemistry from the latter (Frisch 2006; Rivas Plata *et al.* 2010b). *Wirthiotrema* was suggested to belong in a clade together with such morphologically disparate genera as *Carbacanthographis*, *Heiomasia*, *Nadvornikia*, and *Topeliopsis* (Nelsen *et al.* 2010; Rivas Plata & Lumbsch 2011a, b); this clade is possibly related to the *Thelotrema* clade. The latter includes the genus *Leucodecton*, which agrees with *Wirthiotrema* in the paraplectenchymatous excipulum and stictic acid chemistry but usually lacks a dense cortex and the ascospores are of a different type, usually with rather thick walls and often amyloid (Frisch 2006; Rivas Plata *et al.* 2010b). The species of *Wirthiotrema* are found in the shady understory of wet tropical rain forests (Rivas Plata *et al.* 2008).

Key to the species of *Wirthiotrema* found or expected in Costa Rica (5)

1. Ascospores colourless 2
- Ascospores brown 4

2. Norstictic acid ..... ***W.* aff. *glaucopallens***
- Stictic acid 3

3. Excipulum free, forming distinct double margin ..... ***W. duplomarginatum***
- Excipulum more or less fused, not forming a distinct double margin ..... ***W. glaucopallens***

4. Hymenium inspersed ..... ***W. trypaneoides***
- Hymenium clear ..... ***W. desquamans***

Wirthiotrema desquamans (Müll. Arg.) Lücking, *comb. nov.* (Fig. 36A)

MycoBank #800228

Anthracothecium desquamans Müll. Arg., Flora 71: 48 (1888); *Leptotrema desquamans* (Müll. Arg.) Patw. & Makhija, Patwardhan & Makhija, Bryologist 83: 368 (1980); *Myriotrema desquamans* (Müll.Arg.) Hale, Mycotaxon 11: 13 (1980). Lectotype (Patwardhan & Makhija, 1980: 368): Australia, *Berthoud s.n.* (G!).
Thelotrema irosinum Vain., Ann. Acad. Sci. Fenn., Ser. A, 15(6): 174 (1921); *Leptotrema irosinum* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 635 (1923). Lectotype (Hale 1981: 278): Philippines, *Elmer 14749* (TUR-VAIN 26766!).

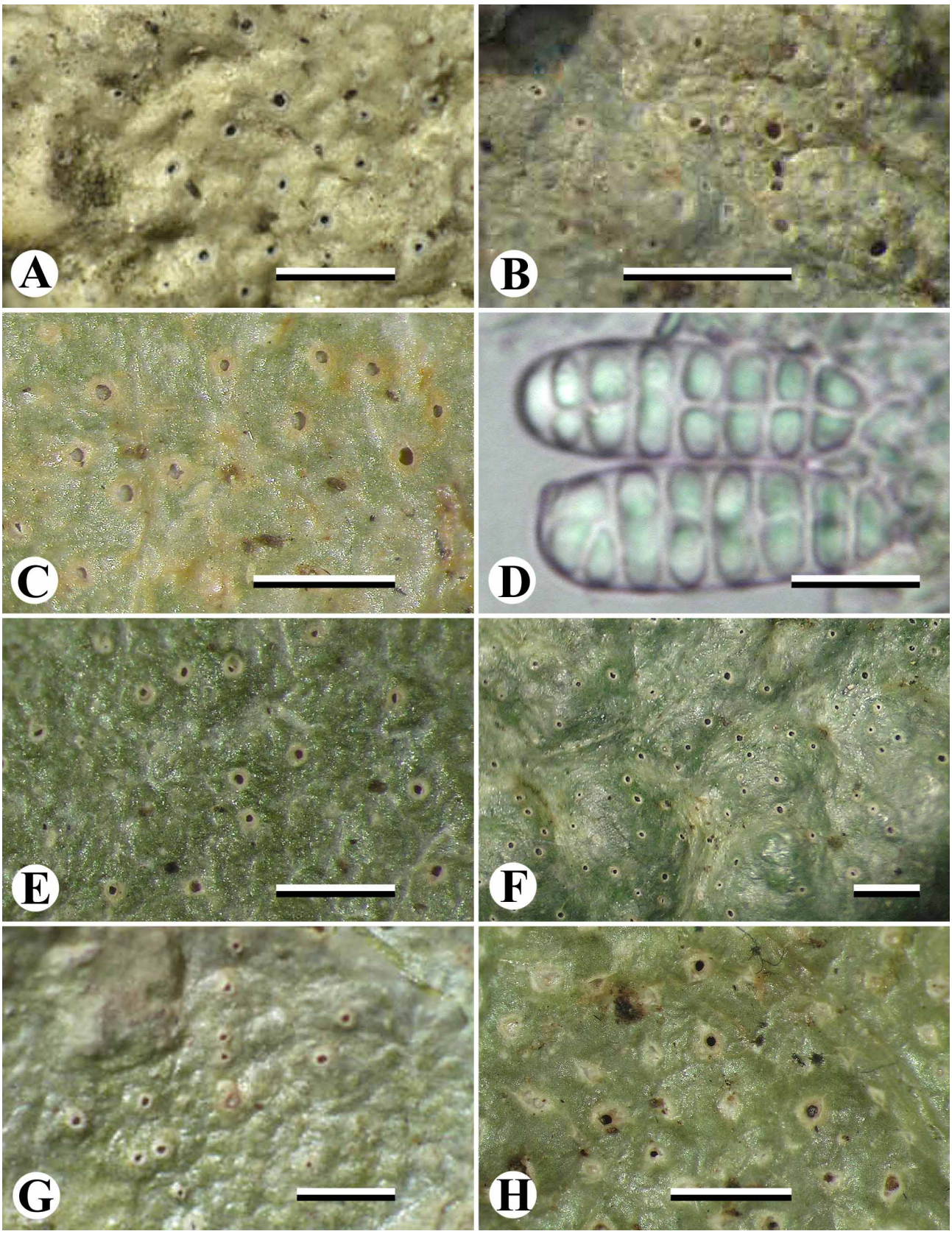

FIGURE 36. A. *Wirthiotrema desquamans*. B–D. *Wirthiotrema duplomarginata*. E–F. *Wirthiotrema glaucopallens*. G. *Wirthiotrema* aff. *glaucopallens*. H. *Wirthiotrema trypaneoides*. Scale = 1 mm except D = 10 µm.

Thallus light grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.2–0.4 mm diam.; disc concealed; margin entire, red-brown. Columella absent. Excipulum paraplectenchymatous, red-brown; periphysoids absent. Hymenium clear. Ascospores 8/ascus, 20–35 × 10–18 µm, ellipsoid, muriform, with slightly thickened septa and angular lumina, brown, I– (non-amyloid). Secondary chemistry: stictic, constictic, hypoconstictic, cryptostictic, and hypostictic acids.

Remarks:—This species is close to *Wirthiotrema trypaneoides* and differs from the latter chiefly in the clear hymenium. Similar species of *Leucodecton* can usually be distinguished by their loose cortex, with the exception of *Leucodecton compunctum* which agrees in many ways with *W. desquamans* except that its ascospores are thick-walled and I+ when young. It also differs in chemistry; Rivas Plata *et al.* (2010a) erroneously keyed *Leucodecton compunctum* out as having stictic acid, but the lectotype actually contains no substances (Frisch 2006).

Specimens examined:—COSTA RICA. Limón: Caribbean coast, Cahuita; 9° 44' N, 82° 50' W, 50 m; cacao plantation SW of the village; on *Theobroma* branches; Jan 1979, *Sipman 12285* (U). Puntarenas: Cordillera de Tilaran, Monteverde, near the cheese factory; 10° 18' N, 84° 49' W, 1450 m; premontane rain forest zone, forest relics among pasturefields, on trunks; Jan 1979, *Sipman 12084* (U), *12113* (U), *12115* (U). Manuel Antonio National Park, near Quepos; 9° 23' N, 84° 09' W, sea level; scattered trees around hotel at end station of bus line; Nov 1988, *Sipman 42313* (B, CR).

Wirthiotrema duplomarginatum* Lücking, Mangold & Lumbsch, *spec. nov. (Fig. 36B–D)
MycoBank #800104

Differing from *Wirthiotrema glaucopallens* in the free excipulum (double margin) with indistinct periphysoids.

Holotype:—AUSTRALIA. Queensland, Cape Kimberley, Cape Tripulation area; *Lumbsch & Mangold 19167c* (F).

Thallus light grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed to erumpent, rounded, 0.2–0.4 mm diam.; disc covered by 0.1–0.2 mm wide pore; proper margin entire, yellowish white, thalline margin entire to fissured, with split inbetween (double margin). Columella absent. Excipulum paraplectenchymatous, pale yellowish to orange-brown; periphysoids present in upper part but indistinct and conclutinated. Hymenium clear. Ascospores 8/ascus, 20–35 × 7–10 µm, ellipsoid, muriform, with slightly thickened septa and angular lumina, colorless, I– (non-amyloid). Secondary chemistry: stictic, constictic, α-acetyl-constictic, α-acetyl-hypoconstictic, and cryptostictic acids.

Remarks:—This new species agrees in most features with *Wirthiotrema glaucopallens* except for the distinctly free excipulum creating a double margin and the periphysoids which are, however, indistinct. The type material and other Australian collections were identified with *Thelotrema myriocarpum* Fée (Mangold *et al.* 2009) which is broadly similar but has a thinner, less glossy thallus and larger, more *Thelotrema*-like apothecia. The main difference, however, are the ascospores. The Australian and Costa Rica material have ascospores of a type identical with *Wirthiotrema glaucopallens*, with rounded ends and only slightly thickened septa and angular lumina that are very regularly arranged like a brick wall, and thin outer walls. The type of *Thelotrema myriocarpum*, in contrast, has *Thelotrema*-like ascospores with tapering ends, thin septa, and thick outer wall. Because of the very characteristic ascospores and the general appearance, the new species is placed in *Wirthiotrema*, even if the presence of periphysoids would speak against such a placement. However, other related genera in the *Topeliopsis* clade do include species with periphysoids, so a species of *Wirthiotrema* with periphysoids is not unexpected.

Additional specimens examined (paratypes):—AUSTRALIA. Queensland: Cape Kimberley, Cape Tripulation area; *Lumbsch & Mangold 19120dB, 19120l, 19167r* (F).

COSTA RICA. Guanacaste: Cacao Biological Station (Guanacaste Conservation Area); 10° 56' N, 85° 28' W, 1000 m; epiphyte in humid primary montane forest near the station; Jun 1995, *Sipman 37294* (B, CR).

***Wirthiotrema glaucopallens* (Nyl.) Rivas Plata & Kalb** (Fig. 36E–F)

Wirthiotrema glaucopallens (Nyl.) Rivas Plata & Kalb in Rivas Plata *et al.*, Lichenologist 42: 201 (2010); *Thelotrema glaucopallens* Nyl., Ann. Sci. Nat., Bot., Ser. 4, 19: 327 (1863). Lectotype (Hale 1974: 35): Cuba, *Wright s.n.* (FH!; isolectotypes: H-NYL 22598!; M!, UPS!; Wright, Lich. Cub. 28).

Thelotrema pechuelii Müll. Arg., Linnaea 34: 34 (1880). Holotype: Congo, *Pechuel-Loesche 300 p.p.* (G!).

Thelotrema homopastoides Vain., J. Bot. 34: 207 (1896); *Thelotrema glaucopallens* var. *homopastoides* (Vain.), Ann. Acad. Sci. Fenn., Ser. A, 6(7): 138 (1915). Lectotype (Hale 1974: 35: Lesser Antilles (St. Vincent), *Elliott 244* (TUR-VAIN 26845!; isolectotype: BM!).

Thelotrema butuanum Vain., Ann. Acad. Sci. Fenn., ser. A 15(6): 183 (1921). Lectotype (Hale 1974: 35): Philippines, *Fénix 28347 p.p.* (W!; isolectotype: TUR-VAIN 26851!).

Thallus light grey-olive, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia immersed to erumpent, rounded, 0.3–0.5 mm diam.; disc mostly covered by 0.1–0.2 mm wide pore; margin entire, pale brown. Columella absent. Excipulum paraplectenchymatous, brown; periphysoids absent. Hymenium clear. Ascospores 8/ascus, 20–30 × 9–15 µm, ellipsoid, muriform, with slightly thickened septa and angular lumina, colorless, I– (non-amyloid). Secondary chemistry: stictic, constictic, α-acetyl-constictic, consalazinic, and sometimes menegazziaic acids.

Remarks:—*Wirthiotrema glaucopallens* is the most common and widespread species in the genus. It is recognized by the combination of glossy, corticate thallus, myriotremoid apothecia, non-amyloid muriform ascospores with only slightly thickened septa, and stictic acid.

Specimens examined:—COSTA RICA. Alajuela: San Ramón Forest Reserve, near station at Río Lorencito, 5 km NE of Cerro Jabonal; 10° 13' N, 84° 37' W, 1000 m; humid, mossy forest with many ferns on mountain ridge, on thin trunk in undergrowth; Nov 1988, *Sipman et al. 41985* (B, CR). Limón: Hitoy Cerere Biological Reserve, Hitoy Cerere Biological Station (La Amistad Caribe Conservation Area), Talamanca Ridge, 125 km ESE of San José, 40 km S of Limón, near Pandora, trail along Río Estrella to waterfall; 83° 02' W, 9° 40' N, 150 m; lowland to lower montane rain forest zone, secondary vegetation and disturbed primary forest along river, on bark (lower trunk), fully shaded; Mar 2004, *Aptroot 60139* (BR, INB); ibid., on bark (trunk base), partially shaded; Mar 2004, *Lücking 17064* (CR, F, , USJ); ibid., on bark (lower trunk), partially shaded; Mar 2004, *Sipman 51623, 51630* (B, INB); ibid., on bark (lower trunk), fully shaded; Mar 2004, *Aptroot 60175, 60199* (BR, INB). Puntarenas: Carara National Park, Quebrada Bonita Section (Pacífico Central Conservation Area), 60 km WSW of San Jose on road from Orotina to Quepos (34), trail from visitor's center to Quebrada Bonita; 84° 35' W, 9° 47' N, 100 m; lowland moist forest zone, partly disturbed dense primary forest with understory dominated by *Erythrochiton gymnanthus*, on bark (lower stem), fully shaded; Jul 2002, *Lücking 15620* (F). Carara Biological Reserve, 15 km SSW of Orotina; 9° 47' N, 84° 37' W, 50 m; disturbed primary, 40 m tall forest, along trail near warden's house, on fallen tree; Nov 1988, *Sipman & Döbbeler 42240* (B, CR), *42244* (B, CR). Manuel Antonio National Park, near Quepos; 9° 23' N, 84° 09' W, sea level; scattered trees around hotel at end station of bus line; Nov 1988, *Sipman 42314* (B, CR). Corcovado National Park, Los Patos Section, Los Patos Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 40 km WSW of Golfito, access trail to station and first, hilly part (5 km) of trail to Sirena; 83° 29' W, 8° 34' N, 100–300 m; lowland rain forest zone, closed primary forest, on bark (trunk base), exposed; Apr 2003, *Buck 44077* (INB, NY); ibid., Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, round trail NW of station (Sendero Sirena and Sendero Guanacaste); 83° 35' W, 8° 29' N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (lower stem), partially

shaded; Apr 2003, *Lücking 16201* (F, INB); ibid., second part of trail from Los Patos to Sirena station; 83° 33' W, 8° 32' N, sea level; lowland rain forest zone, oldgrowth secondary forest and closed secondary vegetation, on bark (lower stem), semi-exposed; Apr 2003, *Sipman 51093* (B, INB); ibid., , round trail NW of station (Sendero Sirena and Sendero Guanacaste); 83° 35' W, 8° 29' N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (lower stem), partially shaded; Apr 2003, *Lücking 16251a* (F). Wilson Botanical Garden, Las Cruces Biological Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 190 km SE of San José, trail beyond botanical garden; 82° 58' W, 8° 47' N, 1200 m; montane rain forest zone, primary forest, on bark (lower trunk), fully shaded; Sep 2007, *Lücking 21082* (F).

Wirthiotrema aff. *glaucopallens* (Nyl.) Rivas Plata & Kalb (Fig. 36G)

Remarks:—This material differs from *Wirthiotrema glaucopallens* in having norstictic acid as the main substance. Similar species with the same chemistry include *M. norsticticum* (see above), which has much smaller, strongly amyloid ascospores, and *Thelotrema canarense* Patw. & C. Kulk., which agrees in ascospore size but lacks a dense cortex and the ascospores are amyloid. We have refrained from formally recognizing this material as new species since the available specimens are small.

Specimens examined:—COSTA RICA. Puntarenas: Carara National Park, Quebrada Bonita Section (Pacífico Central Conservation Area), 60 km WSW of San Jose on road from Orotina to Quepos (34), trail from visitor's center to Quebrada Bonita; 84° 35' W, 9° 47' N, 100 m; lowland moist forest zone, partly disturbed dense primary forest with understory dominated by *Erythrochiton gymnanthus*, on bark (lower stem), fully shaded; Jul 2002, *Sipman 48389b* (B, INB). Corcovado National Park, Sirena Section, Sirena Biological Station (Osa Conservation Area), Osa Pensinsula, 160 km SSE of San José and 50 km WSW of Golfito, round trail NW of station (Sendero Sirena and Sendero Guanacaste); 83° 35' W, 8° 29' N, sea level; lowland and coastal rain forest zone, oldgrowth coastal secondary forest and primary forest remnants on sandy soil, on bark (lower stem), partially shaded; Apr 2003, *Sipman 51166* (B, CR), *51172a* (B, INB).

Wirthiotrema trypaneoides (Nyl.) Rivas Plata & Lücking (Fig. 36H)

Wirthiotrema trypaneoides (Nyl.) Rivas Plata & Lücking in Rivas Plata *et al.*, Lichenologist 42: 201 (2010); *Thelotrema trypaneoides* Nyl., Ann. Sci. Nat., Bot., Sér. 4, 19: 335 (1863); *Leptotrema trypaneoides* (Nyl.) Riddle, Bull. Torrey Bot. Club 43: 151 (1916); *Myriotrema trypaneoides* (Nyl.) Hale, Mycotaxon 11: 135 (1980). Lectotype (Hale 1978: 54): Cuba, *Wright 156* (FH!; isolectotypes: BM!, G!, PC!, UPS!, US!).

Thelotrema subterebrans Nyl., Flora 59: 561 (1876); *Leptotrema subterebrans* (Nyl.) Zahlbr., Cat. Lich. Univ. 2: 640 (1923). Lectotype (Hale 1978: 55): Cuba, *Wright 520* (H-NYL 22514!).

Thelotrema laevius Vain., J. Bot. 34: 207 (1896); *Leptotrema laevius* (Vain.) Zahlbr., Cat. Lich. Univ. 2: 635 (1923). Holotype: Lesser Antilles (St. Vincent), *Elliott s.n.* (TUR-VAIN 26774!).

Thallus light grey-green, smooth to uneven, with dense, prosoplectenchymatous cortex with internal splitting; photobiont layer and medulla with clusters of calcium oxalate crystals. Apothecia erumpent, rounded, 0.2–0.5 mm diam.; disc covered by narrow, 0.05–0.1 mm wide pore; margin entire, yellowish white. Columella absent. Excipulum paraplectenchymatous, pale orange-brown; periphysoids absent. Hymenium inspersed. Ascospores 8/ascus, 25–40 × 5–15 µm, ellipsoid, muriform, with thickened septa and angular to rounded lumina, brown, I– (non-amyloid). Secondary chemistry: stictic, constictic, hypoconstictic, cryptostictic, and hypostictic acids.

Remarks:—*Wirthiotrema trypaneoides* is unusual in the genus in having an inspersed hymenium and dark brown ascospores with comparatively thick septa and rounded lumina. Nevertheless, Australian specimens (Mangold *et al.* 2009) that were sequenced cluster with the other *Wirthiotrema* species (Rivas Plata

et al. 2010a). Most similar is *W. desquamans* which has a clear hymenium and smaller ascospores with thinner septa.

Specimens examined:—COSTA RICA. Guanacaste: Cacao Biological Station (Guanacaste Conservation Area); 10° 56' N, 85° 28' W, 1000 m; epiphyte in humid primary montane forest near the station; Jun 1995, *Sipman 37286* (B, CR). Limón: Hitoy Cerere Biological Reserve, Hitoy Cerere Biological Station (La Amistad Caribe Conservation Area), Talamanca Ridge, 125 km ESE of San José, 40 km S of Limón, near Pandora, trail adjacent to access road before station; 83° 02' W, 9° 40' N, 150–200 m; lowland to lower montane rain forest zone, disturbed primary and oldgrowth secondary forest, on bark (lower trunk), semi-exposed; Mar 2004, *Lücking 17046a* (F, USJ). Puntarenas: Carara National Park, Quebrada Bonita Section (Pacífico Central Conservation Area), 60 km WSW of San Jose on road from Orotina to Quepos (34), trail from visitor's center to Quebrada Bonita; 84° 35' W, 9° 47' N, 100 m; lowland moist forest zone, partly disturbed dense primary forest with understory dominated by *Erythrochiton gymnanthus*, on bark (trunk, fallen), Jul 2002, *Lücking 15613a* (F, INB, USJ). Marenco Biological Reserve, Marenco Station (Osa Conservation Area), Drake Bay,150 km SSE of San José and 50 km WSW of Golfito, beach trail; 83° 40' W, 8° 43' N, sea level; lowland coastal rain forest zone, coastal rain forest, on bark (lower trunk), fully shaded; Feb 1997, *Lücking 97-263* (F). Wilson Botanical Garden, Las Cruces Biological Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 190 km SE of San José, trail beyond botanical garden; 82° 58' W, 8° 47' N, 1200 m; montane rain forest zone, primary forest, on bark (lower trunk), fully shaded; Sep 2007, *OTS course P1-MR* (F).

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Appendix: Voucher information for specimens depicted in Figures 5–36.

FIGURE 5.
A. *Acanthotrema bicellularis*. Holotype.
B–C. *Acanthotrema brasilianum*. B, Costa Rica, Chaves 2351; C, Costa Rica, Sipman 53247.
D. *Acanthotrema kalbii*. Holotype.
E. *Ampliotrema amplius*. Costa Rica, Lücking 16300a.
F. *Ampliotrema auratum*. Brazil, Cáceres 901.
G. *Ampliotrema cocosense*. Holotype.
H. *Ampliotrema dactylizum*. Costa Rica, Grube 11455.

FIGURE 6.
A. *Ampliotrema discolor*. Costa Rica, Lücking 16309g.
B. *Ampliotrema lepadinoides*. Costa Rica, Lücking 16311b.
C. *Ampliotrema palaeoamplius*. Costa Rica, Nelsen 3567E.
D. *Ampliotrema panamense*. Holotype.
E. *Ampliotrema* aff. *panamense*. Costa Rica, Sipman 37292.
F. *Chapsa albida*. Holotype.
G. *Chapsa alborosella*. Costa Rica, Lücking 00-245.
H. *Chapsa astroidea*. Costa Rica, Lücking 16392e.

FIGURE 7.
A. *Chapsa chionostoma*. Lectotype of *Ocellularia phlyctellacea*.
B. *Chapsa defecta*. Holotype.
C. *Chapsa defectosorediata*. Holotype.
D. *Chapsa dilatata*. Costa Rica, Sipman 12085.
E. *Chapsa discoides*. Costa Rica, Lücking 17650a.
F. *Chapsa dissuta*. Panama, Hale 43424.
G. *Chapsa esslingeri*. Holotype.
H. *Chapsa farinosa*. Holotype.

FIGURE 8.
A. *Chapsa hiata*. Holotype.
B. *Chapsa laceratula*. Costa Rica, Lücking 16365a.
C. *Chapsa lassae*. Costa Rica, Lizano PR-9-9.
D. *Chapsa leprieurii*. Costa Rica, Lücking 00-239.
E. *Chapsa leprocarpa*. Isotype.
F–H. *Chapsa meridensis*. Costa Rica, Lücking 17700.

FIGURE 9.
A. *Chapsa neei*. Costa Rica, Dodge 10073.
B. *Chapsa perdissuta*. Costa Rica, Lücking 17306.
C. *Chapsa phlyctidioides*. Costa Rica, Lücking 17260.
D. *Chapsa platycarpa*. Costa Rica, Sipman 37279.
E. *Chapsa platycarpella*. Costa Rica, Lücking 17267d.
F. *Chapsa pseudoschizostoma*. Holotype.
G. *Chapsa referta*. Costa Rica, Buck 2943.
H. *Chapsa stellata*. Holotype.

FIGURE 10.
A–B. *Chapsa sublilacina*. Costa Rica, Lücking 16239.
C–E. *Chapsa sublilacina var. cyanea*. Holotype.
F–H. *Chapsa thallotrema*. F–G, Holotype; H, Costa Rica, Lücking 17219.

FIGURE 11.
A. *Chroodiscus argillaceus*. Cocos Island, Lücking sn.
B. *Chroodiscus australiensis*. Costa Rica, Lücking 00-234.
C. *Chroodiscus coccineus*. Costa Rica, Lücking 2511.
D. *Chroodiscus neotropicus*. Costa Rica, Lücking 1591.
E. *Chroodiscus submuralis*. Holotype.
F. *Clandestinotrema analorenae*. Holotype.
G. *Clandestinotrema antoninii*. Costa Rica, Lücking 38947.
H. *Clandestinotrema clandestinum*. Costa Rica, Aptroot 60624.

FIGURE 12.
A. *Clandestinotrema erumpens*. Isotype.
B. *Clandestinotrema leucomelaenum*. Costa Rica, Sipman 48040a.
C. *Clandestinotrema pauperius*. Isotype.
D. *Clandestinotrema stylothecium*. Costa Rica, Lücking 17321b.
E. *Clandestinotrema tenue*. Costa Rica, Lücking 97-39.
F. *Cruentotrema cruentatum*. Brazi, Cáceres 1070.
G. *Diploschistes cinereocaesius*. Costa Rica, Lücking 15540.
H. *Diploschistes muscorum subsp. bartlettii*. Costa Rica, Lücking sn.

FIGURE 13.
A. *Diploschistes scruposus*. Costa Rica, Lücking sn.
B. *Enigmotrema rubrum*. Holotype.
C. *Fibrillithecis confusa*. Costa Rica, Lücking 17322.
D. *Fibrillithecis pachystoma*. Colombia, Lindig 55.
E. *Gyrotrema aurantiacum*. Holotype.
F. *Gyrotrema papillatum*. Holotype.
G–H. *Gyrotrema wirthii*. G, Costa Rica, Lücking 16252b; H, Costa Rica, Lücking 16241.

FIGURE 14.
A–B. *Leptotrema wightii*. Costa Rica, Nelsen 2034A.
C. *Leucodecton album*. Holotype.
D. *Leucodecton bisporum*. Costa Rica, Nelsen 3271F.
E. *Leucodecton compunctellum*. Australia, Streimann 46018.
F. *Leucodecton compunctum*. Holotype.
G. *Leucodecton expallescens*. Costa Rica, Lücking 15123.
H. *Leucodecton fissurinum*. Costa Rica, Sipman 37288.

FIGURE 15.
A. *Leucodecton glaucescens*. Costa Rica, Lücking 6696.
B. *Leucodecton occultum*. Costa Rica, Lücking 16100a.
C. *Leucodecton sordidescens*. Costa Rica, Sipman 42270a.
D. *Leucodecton subcompunctum*. Lectotype.
E. *Melanotrema meiospermum*. Indonesia, Groenhart 7297.
F. *Melanotrema platystomum*. Costa Rica, Chaves 2353.
G. *Myriotrema aggregans*. Holotype.
H. *Myriotrema album*. Australia, Streimann 57668.

FIGURE 16.
A. *Myriotrema clandestinoides*. Holotype.

B. *Myriotrema clandestinum*. Costa Rica, Chaves sn.
C–E. *Myriotrema classicum*. Holotype.
F. *Myriotrema concretum*. Costa Rica, Sipman 46562.
G. *Myriotrema congestum*. Holotype.
H. *Myriotrema costaricense*. Costa Rica, Lücking 20142.

FIGURE 17. A–B. *Myriotrema endoflavescens*. Holotype.
C. *Myriotrema frondosolucens*. Holotype.
D. *Myriotrema glaucophaenum*. Costa Rica, Aptroot 60863.
E. *Myriotrema glauculum*. Isotype of *Thelotrema leptosporum*.
F. *Myriotrema hartii*. Costa Rica, Sipman 44331.
G. *Myriotrema laeviusculum*. Costa Rica, OTS P5-rm.
H. *Myriotrema microporellum*. Isotype.

FIGURE 18.
A. *Myriotrema microporum*. Costa Rica, Lücking 16104.
B. *Myriotrema myrioporoides*. Brazil, Cáceres 576.
C. *Myriotrema myriotremoides*. Costa Rica, Sipman 42378.
D. *Myriotrema neofrondosum*. Venezuela, Galiz 45b.
E. *Myriotrema norsticticum*. Holotype.
F. *Myriotrema olivaceum*. Costa Rica, Sipman 12238.
G. *Myriotrema plurifarium*. Lectotype.
H. *Myriotrema pulverulentum*. Holotype.

FIGURE 19.
A. *Myriotrema subconforme*. Costa Rica, Dodge 7406.
B. *Myriotrema thailandicum*. Costa Rica, Filson 16379.
C. *Myriotrema uniseptatum*. Panama, Hale 47678.
D–E. *Myriotrema viridialbum*. D, Costa Rica, Sipman 12256; E, Isotype.
F–H. *Nadvornikia hawaiiensis*. Costa Rica, Dodge 7826.

FIGURE 20.
A. *Ocellularia albobullata*. Holotype.
B. *Ocellularia albocincta*. Costa Rica, Sipman 46553.
C. *Ocellularia antillensis*. Costa Rica, Lücking 00-153.
D. *Ocellularia ascidioidea*. Costa Rica, Sipman 50984.
E. *Ocellularia aurulenta*. Panama, Hale 43467.
F. *Ocellularia bahiana*. Costa Rica, Lücking 15075.
G. *Ocellularia barroensis*. Costa Rica, Lücking 00-250.
H. *Ocellularia calvescens*. Costa Rica, Sipman 51984.

FIGURE 21.
A. *Ocellularia cavata*. Brazil, Cáceres 557.
B. *Ocellularia chiriquiensis*. Holotype.
C–D. *Ocellularia cocosensis*. Holotype.
E. *Ocellularia conformis*. Isolectotype.
F. *Ocellularia crocea*. Panama, Hale 43591.
G–H. *Ocellularia cryptica*. G, Paratype; H, Holotype.

FIGURE 22.
A. *Ocellularia decolorata*. Holotype.
B. *Ocellularia dolichotata*. Costa Rica, Buck 44104.
C. *Ocellularia domingensis*. Costa Rica, Lücking 21078.
D. *Ocellularia fecunda*. Isolectotype.
E. *Ocellularia flavoperforata*. Holotype.
F. *Ocellularia gerardii*. Holotype.
G–H. *Ocellularia globifera*. Holotype.

FIGURE 23.
A. *Ocellularia inspersata*. Holotype.
B. *Ocellularia inspersula*. Holotype.
C. *Ocellularia interposita*. Costa Rica, Lücking 00-154.
D. *Ocellularia inturgescens*. Costa Rica, Sipman 44329.
E–F. *Ocellularia isohypocrellina*. E, Holotype; F, Paratype.
G. *Ocellularia laevigatula*. Holotype.
H. *Ocellularia laeviusculoides*. Holotype.

FIGURE 24.
A. *Ocellularia landronii*. Brazil, Cáceres 105.
B. *Ocellularia mauritiana*. Holotype.
C. *Ocellularia maxima*. Panama, Hale 43541.
D. *Ocellularia minutula*. Costa Rica, Sipman 42270.
E. *Ocellularia mordenii*. Costa Rica, Grube 11442.
F. *Ocellularia obturascens*. Costa Rica, Dodge 7828.
G. *Ocellularia papillata*. Costa Rica, OTS P1-rb.
H. *Ocellularia perforata*. Lectotype.

FIGURE 25.
A. *Ocellularia pluriporoides*. Costa Rica, Lücking 16359a.
B. *Ocellularia praestans*. Costa Rica, Sipman 37290.
C. *Ocellularia praestantoides*. Holotype.
D. *Ocellularia pseudopyrenuloides*. Holotype.
E. *Ocellularia psorbarroensis*. Holotype.
F. *Ocellularia rhabdospora*. Puerto Rico, Sipman 26016.
G. *Ocellularia rhodostroma*. Costa Rica, Sipman 37289.
H. *Ocellularia ripleyi*. Costa Rica, Lücking 17047a.

FIGURE 26.
A. *Ocellularia subcarassensis*. Holotype.
B. *Ocellularia subpraestans*. Costa Rica, Lücking 16233g.
C–D. *Ocellularia subpyrenuloides*. Holotype.
E. *Ocellularia supergracilis*. Holotype.
F. *Ocellularia tacarcunae*. Holotype.
G. *Ocellularia terebrata*. Costa Rica, Lücking sn.
H. *Ocellularia terrabensis*. Holotype.

FIGURE 27.
A. *Ocellularia umbilicata*. Costa Rica, Lücking 16572.
B. *Ocellularia urceolaris*. Costa Rica, Lücking 15114a.
C. *Ocellularia vezdana*. Isotype.
D–E. *Ocellularia violacea*. D, Costa Rica, Lücking 17261b; E, Lectotype.
F. *Ocellularia viridis*. Costa Rica, Sipman 47813d.
G. *Ocellularia xanthostroma*. Costa Rica, Lücking 97-249.
H. *Ocellularia zamorana*. Holotype.

FIGURE 28.
A. *Pycnotrema pycnoporellum*. Costa Rica, Lücking 17008.
B. *Redingeria glyphica*. Lectotype.
C. *Redingeria leiostoma*. Lesser Antilles, Imshaug 24859.
D. *Redingeria microspora*. Costa Rica, Lücking 16110.
E. *Redingeria vulcani*. Panama, Hale 44763.
F. *Reimnitzia santensis*. Costa Rica, Dodge 6633.
G. *Schizotrema cryptotrema*. Costa Rica, Aptroot 60884.
H. *Schizotrema guadeloupense*. Costa Rica, Sipman 20875.

FIGURE 29.
A–B. *Stegobolus anamorphoides*. A, Costa Rica, Lücking 97-247; B, Costa Rica, Lücking sn.
C. *Stegobolus anamorphus*. Costa Rica, Lücking sn.
D. *Stegobolus auberianus*. Costa Rica, Lücking 97-244.
E–F. *Stegobolus berkeleyanus*. Costa Rica, Standley & Valerio 48501.
G. *Stegobolus crassus*. Costa Rica, Lücking 15102b.
H. *Stegobolus emersus*. Costa Rica, Lücking 16243b.

FIGURE 30.
A. *Stegobolus fissus*. Lectotype.
B. *Stegobolus granulosus*. Costa Rica, Lücking 97-107.
C. *Stegobolus isidiiferus*. Costa Rica, Lücking 16248.
D. *Stegobolus lankaensis*. Costa Rica, Lücking 16236b.
E. *Stegobolus metaphoricus*. Costa Rica, Dodge 7264.
F. *Stegobolus percolumellatus*. Costa Rica, Lücking 97-251.
G. *Stegobolus radians*. Brazil, Cáceres 2071.
H. *Stegobolus reconditus*. Holotype.

FIGURE 31.
A. *Stegobolus subcavatus*. Holotype of *Thelotrema vagum*.
B. *Stegobolus subemersus*. Costa Rica, Dodge 7831.
C. *Stegobolus wrightii*. Costa Rica, Lücking 16236a.
D. *Thelotrema adjectum*. Isotype.
E. *Thelotrema* aff. *adjectum*. Costa Rica, Aptroot 60508.
F. *Thelotrema conveniens*. Colombia, Lindig sn.
G. *Thelotrema diplotrema*. Costa Rica, Lücking 17220.
H. *Thelotrema gomeziana*. Holotype.

FIGURE 32.
A. *Thelotrema hypoprotocetraricum*. Holotype.
B. *Thelotrema lacteum*. Costa Rica, Sipman 48045e.
C. *Thelotrema lepadinum*. Costa Rica, Navarro 1749.
D. *Thelotrema lepadodes*. Costa Rica, Lücking 97-128.
E. *Thelotrema monosporum*. Costa Rica, Lücking sn.
F. *Thelotrema myriocarpum*. Isotype.
G–H. *Thelotrema pachysporum*. G, Florida, Lücking 26568a; H, Costa Rica, Sipman 53333.

FIGURE 33.
A. *Thelotrema porinoides*. Costa Rica, Will-Wolf 12746a.
B–D. *Thelotrema submyriocarpum*. Holotype.
E. *Thelotrema subtile*. Lectotype.
F. *Thelotrema suecicum*. Costa Rica, Sipman 48129.
G–H. *Thelotrema wilsonii*. G, Costa Rica, Lücking 97-117; H, Costa Rica, Nash 41600.

FIGURE 34.
A–B. *Thelotrema defossum*. Holotype.
C–D. *Thelotrema demersum*. Holotype
E–H. *Thelotrema jugale*. E–G, Holotype of *Ocellularia jugalis*; G–H, holotype of *Thelotrema pseudosubtile*.

FIGURE 35.
A. *Thelotrema lathraeum*. Florida, Common 7371A.
B. *Thelotrema parvizebrinum*. Holotype.
C. *Thelotrema petractoides*. Holotype.
D–E. *Thelotrema subtile*. D, Lectotype of *Thelotrema subtile*; E, Holotype of *Ocellularia bonplandii* var. *obliterata*.
F. *Thelotrema suecicum*. Lectotype.
G–H. undescribed species of *Thelotrema* from Australia, Mangold 3p.

FIGURE 36.
A. *Wirthiotrema desquamans*. Costa Rica, Sipman 42313.
B–D. *Wirthiotrema duplomarginata*. Costa Rica, Sipman 37294.
E–F. *Wirthiotrema glaucopallens*. Costa Rica, Lücking 17064, 21082.
G. *Wirthiotrema* aff. *glaucopallens*. Costa Rica, Sipman 51166.
H. *Wirthiotrema trypaneoides*. Costa Rica, Lücking 00-263.