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A Review of the Lichens of the Dare Regional Biodiversity Hotspot in the Mid-Atlantic Coastal Plain of North Carolina, Eastern North America

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ABSTRACT The results of a large-scale biodiversity inventory of lichens (including lichenicolous and allied fungi) in the Dare Regional Biodiversity Hotspot (DRBH) are presented. The DRBH is a region within the Mid-Atlantic Coastal Plain (MACP) of eastern North America that was recently delineated based on its unique and diverse lichen communities relative to other areas of the Atlantic Coast. Drawing on 4,952 newly generated voucher specimens from 49 sites, patterns of biodiversity and biogeography are presented and discussed within the context of both the DRBH and the broader MACP. Relationships between natural communities, vegetation, and lichen communities are discussed, as are threats to the lichen biota. A series of conservation actions are presented together with avenues for future study. In addition, supplementary resources are provided in the form of: (a) a checklist of DRBH lichens, lichenicolous fungi, and allied fungi; (b) keys to DRBH lichens and lichenicolous and allied fungi; and (c) formal descriptions of the following species new to science that were discovered during the inventory: *Albemarlea pamlicoensis* gen. et. sp. nov., *Arthonia agelastica* sp. nov. (on *Lecanora louisianae* B. de Lesd.), *Arthonia hodgesii* sp. nov. (on *Graphis lineola*), *Arthonia stevensoniana* sp. nov. (on *Haematomma accolens*), *Lichenochora haematommum* sp. nov. (on *Haematomma persoonii*), *Megalaria alligatorensis* sp. nov., *Minutoexcipula miniatoexcipula* sp. nov. (on *Pertusaria epixantha*), *Trichosphaerella buckii* sp. nov. (on *Punctelia rudecta*).

Key words: Barrier island, biodiverse understudied groups, bottomland, endemism, obligate symbionts, outer banks, pocosin, sea-level rise, swamp, symbiosis.

INTRODUCTION In 2012, we began a large-scale and systematic inventory of lichen biodiversity in the Mid-Atlantic Coastal Plain (MACP) of eastern North America. The MACP is an ecoregion approximately 89,691 km² (34,630 mi²) in size that comprises the low-lying ecosystems along the Atlantic Coast of the USA from southern New Jersey to northern Florida (US Environmental Protection Agency 1997, Auch 2000). The MACP is recognized as one of the most biologically diverse ecoregions in North America (Hall and Schafale 1999), although its lichen biota had been the subject of little study. Overall, the region has been highly impacted by anthropogenic change (Auch 2000, Loveland and Acevedo 2000, Napton et al. 2010), with nearly a

tenth of the region remaining as “intact natural habitat,” which is increasingly threatened by diverse forces, including fragmentation and loss of remaining habitat by development, increased storm intensity and frequency, overexploitation of timber resources, pollution, and sea level rise (Kirby-Smith and Barber 1979, LeGrande et al. 1992, Bellis 1995, Shankman 1996, Riggs and Ames 2003, Brown et al. 2005, Berman and Berquist 2007, Hupp et al. 2009, Sallenger et al. 2012, Villarini and Vecchi 2012, Lorber and Rose 2015, US Army Corps of Engineers 2015).

Before beginning our inventory of the MACP, we expected, based on experience from previous small-scale efforts in the region, that we would encounter considerable diversity as well as many new and unusual species. However, when we began to inventory the largest remaining contiguous protected areas in the MACP, an

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extensive area of swamps centered in the Albemarle-Pamlico Peninsula of North Carolina, we immediately recognized that the region hosted much higher levels of lichen biodiversity than we had expected. Following two years of field study, we summarized our biodiversity data for the portion of the MACP between southern New Jersey and the North Carolina–South Carolina border. This led to the discovery that all of the most biodiverse sites in that portion of the MACP were concentrated on or near the Albemarle-Pamlico Peninsula, and that they were all within 1 m of current sea levels (Lendemer and Allen 2014). This area largely corresponds to the original extent of the once vast swamp that was historically referred to as the Great Alligator Dismal (e.g., Morse 1804, Cummings 1966). In recognition of the unique lichen communities in the Albemarle-Pamlico Peninsula, we designated the region as the Dare Regional Biodiversity Hotspot (DRBH), a lichen biodiversity reservoir imperiled by sea-level rise and anthropogenic change (Lendemer and Allen 2014).

Recognizing the importance of a thorough understanding of the lichens of the DRBH for the effective conservation of American, let alone global, lichen biodiversity, we held the 23rd Tuckerman Workshop in the region in 2014. Before and during the workshop, we visited additional localities, and considerably increased our knowledge of the known biodiversity. The remarkable increase in DRBH lichen biodiversity found as a result of the Tuckerman meeting convinced us that a summary treatment was needed, and that such a work would be useful to both the lichenological community and, more broadly, to those involved in the biodiversity sciences, as well as conservation and management in the MACP. As such, we undertook the present study, the results of which are presented here.

MATERIALS AND METHODS

Delineation of the Study Area

This study details the results of a large-scale biodiversity inventory of the DRBH (Figure 1A), an area recently designated by Lendemer and Allen (2014) because of its unique and outstandingly diverse lichen communities. The DRBH is located entirely within the North Carolina portion of the EPA Level III Ecoregion the MACP (US Environmental Protection Agency 1997, Auch 2000). The bulk of the DRBH is

comprised of the mainland Albemarle-Pamlico Peninsula, a peninsula bounded to the north by the Albemarle Sound and to the south by the Pamlico Sound, together with the adjacent barrier islands that form a portion of the famous North Carolina Outer Banks. As delineated here, the DRBH also includes the North River drainage, which is an extensive system of swamp forests along the North River just north of the Albemarle-Pamlico Peninsula in mainland Camden and Currituck Counties. Essentially, the DRBH comprises all of the North Carolina counties of Currituck, Dare, Hyde, Tyrrell, and Washington, together with a portion of Camden County located along the North River (Figure 1B). This area encompasses the largest contiguous natural areas in the MACP (Lendemer and Allen 2014) and has a land area 4,501 km² in size, of which 1,604 km² (36%) are protected.

Field Inventory and Herbarium Study

This study is based on a combination of fieldwork completed as part of a lichen biodiversity inventory of the MACP (see Lendemer and Allen 2014), and a large-scale study of existing vouchers deposited in the herbarium of the New York Botanical Garden (NY). Field work was carried out over a series of four trips, beginning with 8–12 December 2012 carried out by J.C.L., R.C.H., and W.R. Buck, followed by 18–19 March 2013 by J.C.L., 23–24 March 2013 by J.C.L., J.L. Allen, and E.A. Tripp, and 18–24 March 2014 by 30+ participants of the Tuckerman Workshop, including all of the individuals of the previous trips. The Tuckerman Workshop is an annual meeting wherein professional, amateur, and student lichenologists spend five days of field and laboratory time inventorying lichen biodiversity of a region of eastern North America as a group.

Field methods followed those outlined by Lendemer and Allen (2014), wherein a team spent 1–2 hr conducting an expert-based inventory using floristic habitat sampling (see Newmaster et al. 2005) within a site (3.43 ± 2.2 ha) delineated in such a way as to be uniform in habitat (i.e., a single vegetation type with uniform elevation). Sites were selected spontaneously in the field based on direct observations of habitat quality and lichen diversity from vehicles during visits to as many protected areas as were allowed by available time and funds. This method of site selection was intentionally nonrandom, because the goal of the inventory



Figure 1. A. Satellite image maps illustrating the study area and surrounding region. B. The counties that make up the study area. C. All georeferenced vouchers available in Consortium of North American Lichen Herbaria as of 2015 that were collected prior to the present study. D. The sites inventoried as part of this study.

was to document as much biodiversity as possible given available time and resources. Thus, the lowest-diversity sites and most degraded habitats were excluded from this study based on the extensive field experience of the two senior authors in conducting large-scale biodiversity inventories.

Teams of approximately equal numbers allocated approximately equal time to inventory across sites. Each member of the team collected a voucher of each taxon that they encountered at each site, with the goals of: (a) comparing the

taxonomic overlap between collectors; (b) including all common species; and (c) capturing the most complete substrate diversity possible for each species. For each voucher, the substrate and microhabitat were recorded in the field, and for each site, the overall vegetation, habitat, and condition of the site were characterized by field observation.

All vouchers were identified using existing published (e.g., Harris 1995) and unpublished (e.g., the keys published herein) resources. Specimens were examined dry using an Olympus

SZ-STB dissecting microscope (Olympus). Thallus anatomy and measurements of microscopic characters were carried out on sections prepared by hand with a razor and mounted in water, viewed using an Olympus BX53 compound microscope equipped with a DP72 digital camera (Olympus) and CellSens imaging software (Olympus). Chemistry was studied with standard spot tests (K, C, P, UV) following Brodo et al. (2001), and with thin-layer chromatography (TLC) using solvents A and C following Culberson and Kristinsson (1970), as modified for the peanut butter jar by Lendemer (2011).

After identification, all specimens were labeled with georeferenced locality data, voucher-specific substrate data, and collection information. They were then digitized in KEMu and assigned unique identifiers in the form of barcodes and electronic record numbers. Data digitization was performed by one individual (J.C.L.) to assure that records were entered uniformly, taxonomic identifiers were kept constant, and that variants of georeferenced locality data were not entered multiple times. During incorporation into the NY herbarium, any existing vouchers from the MACP already in the collection were also examined, the identifications verified, localities georeferenced, and the data digitized. A special effort was also made to locate, identify, curate, and digitize any additional MACP vouchers located in the undetermined material at NY, as well as in unprocessed portions of donated herbaria, including those of J.P. Dey, E. Lay, and C.F. Reed.

Dataset Assembly, Analysis, and Visualization

Data used in analyses were exported from the NY KEMu system as a single CSV file containing all records from North Carolina. A master data file was created from this bulk export by pruning the dataset to include only records of lichens and lichenicolous fungi from MACP counties following US Environmental Protection Agency (1997). The master dataset was then copied and manipulated as follows: (a) individual CSV files were created for each species for use in producing species distribution maps; and (b) the master file was pruned to include only the subset of records from the DRBH. The pruned dataset composed only of DRBH records was then used to generate a taxonomic checklist for the DRBH, and to obtain counts for the number of vouchers (unique herbarium specimens) and

occurrences (locations defined as a unique latitude and longitude point) for each taxon. The DRBH dataset was then further pruned to include only records from sites inventoried by our team as part of the four trips outlined above. This smaller dataset was then used to: (a) obtain taxonomic diversity values (total number of unique taxonomic identifications) for each site; (b) generate a species versus site presence/absence matrix; and (c) generate a species $\times$ collector $\times$ site presence/absence matrix for the subset of sites visited by three team members (J.C.L., R.C.H., and W.R. Buck).

An additional dataset comprising all records from the DRBH available in the Consortium of North American Lichen Herbaria (CNALH) online database was downloaded on 1 June 2015. Nomenclature for the dataset was updated following Esslinger (2014), and the dataset was pruned to contain only prestudy DRBH voucher data as follows: (a) records erroneously included that were not actually from the DRBH were removed; (b) records of vouchers generated as part of this study or by participants during study-related workshops (e.g., the Tuckerman Workshop held in the DRBH in 2014) were removed.

ArcMap 10.0 (ESRI 2011) software was used to plot the coordinates and geospatially visualize data for the purposes of this study. ArcGIS World Imagery baselayer (ArcGIS World Imagery, Redlands, CA) was selected for the map background, with features including 0.3-m resolution imagery in the continental USA. Georeferenced species occurrence data were saved in CSV-formatted files and uploaded to ArcMap. For each set of occurrence data or site coordinates, the geographic coordinate system for the dataset was selected to display the World Geodetic System 1984. The dataset and map layers were then exported and saved as a single shapefile document. Through ArcToolbox: Data Management Tools, the shapefile was projected using North American Lambert Conformal Conic as the output coordinate system. Routine data calculations were performed, summarized, and visualized in Microsoft Excel (Microsoft Inc., Redmond, Washington). Similarity values and other diversity statistics were calculated using EstimateS for Windows (v9.10; see Colwell and Elsensohn 2014) from datasets formatted as tab-delimited TXT files. All datasets used in this study are archived in Dryad as doi 10.5061/dryad.226d0.

RESULTS AND DISCUSSION A total of 49 sites within the DRBH were inventoried for this study (Figure 1D), from which 4,952 voucher specimens were collected, representing 386 taxa. Of these 386 taxa, 8 are described as new to science (Appendix I), and several were previously described as new to science as part of our inventory efforts (Lendemer and Harris 2014a, Lendemer and Goffinet 2015, Lendemer and Harris 2015). An additional 76 pre-existing vouchers from the DRBH were located at NY and also included in the study. The small number of existing vouchers reflects the overall lack of study that much of the MACP had received previously. This is further evidenced by the lack of mainland DRBH collections in the CNALH, where the majority of existing vouchers from outside this project were collected from coastal barrier islands (Figure 1C; and see “Comparison with Existing Data” section below).

A checklist of the lichens and lichenicolous and allied fungi of the DRBH is provided here in Appendix II. To facilitate further study of the DRBH lichen biota, and to improve the usefulness of this contribution, identification keys for the DRBH lichen biota are also provided here in Appendix III. These resources add to the small number of lichen floristic contributions for the MACP (Lendemer and Yahr 2004, Lendemer and Knapp 2007, Hodkinson and Case 2008), and are the first comprehensive taxonomic keys to cover any part of the Coastal Plain of southeastern North America. While an excellent floristic account, including keys, has been published for part of the Coastal Plain in northeastern North America (Brodo 1968), that work did not include the vast majority of the species present in the southeastern Coastal Plain, and is now taxonomically outdated. The results and discussion presented below are grouped by topic and intended to summarize the data generated from our inventory, place them within the context of the DRBH as well as other inventories, and further place the lichen biota of DRBH within the broader context of the MACP and the Atlantic Coastal Plain as a whole.

Overview: Vegetation and Lichen Diversity

The unexpected diversity of lichens and lichen communities found in the DRBH is an excellent illustration of the issues that have traditionally led to the Coastal Plain having been overlooked

as a biodiversity hotspot (Noss et al. 2015). In our case, lichen biodiversity is concentrated in low-lying swamp forests and upland hardwood forests, in contrast to the longleaf pine savannas and wetlands that have been the focus of previous biodiversity conservation efforts in the region (see below). Even after having conducted extensive field studies in the region, it remains surprising to us that so many ecosystems, vegetation types, and lichen species could occur in an area with little topographic relief, and especially one that has been so greatly impacted by centuries of anthropogenic change (LeGrande et al. 1992, US Environmental Protection Agency 1997, Hall and Schafale 1999, Ricketts et al. 1999, Brown et al. 2005). That such heterogeneity and diversity exists in the DRBH, and more broadly within the Coastal Plain, is attributable to a suite of abiotic factors and stochastic events that have resulted in very different environmental conditions (e.g., soil types, hydrological regimes, microclimates) in close proximity and often at small scales (US Environmental Protection Agency 1997). In the case of the DRBH, what at first glance may appear to be a vast monotonous swamp is, upon closer examination, a rich mosaic of varied natural communities at both large and small scales (Lynch and Peacock 1982a, 1982b; LeGrande et al. 1992, US Department of the Interior 2007, 2008, Sorrie 2014a, 2014b).

From the lichen perspective, habitats in the DRBH can be classified into four main types: marshes and other nonforested wetlands; forested wetlands (i.e., swamps); peatlands (i.e., pocosins and Atlantic white cedar forests); and forested uplands. For an excellent summary of the natural communities within these groups, the reader should refer to Schafale and Weakley (1990); however, it should be noted that our four primary habitat types do not correspond directly to those outlined in that work. Rather, we have grouped the narrowly defined natural communities of Schafale and Weakley (1990) into broad groups (e.g., their eight pocosin and peatland communities are here treated collectively as “peatlands” with two main types). Refer to Table 1 for a comparison of the DRBH natural communities recognized here and those defined by Schafale and Weakley (1990).

Marshes and other nonforested wetlands are biologically productive, important habitats and

Table 1. Comparison of Dare Regional Biodiversity Hotspot natural communities defined by Schafale and Weakley (1990) to those discussed in the present study.

This Study	Schafale & Weakley (1990)		
	Natural Community	System	Grouping
Peatland (Pocosin)	Low pocosin	Palustrine system	Pocosin and peatland communities of the coastal plain
	High pocosin	Palustrine system	Pocosin and peatland communities of the coastal plain
	Pond pine woodland	Palustrine system	Pocosin and peatland communities of the coastal plain
Peatland (Atlantic White Cedar)	Peatland Atlantic white cedar forest	Palustrine system	Pocosin and peatland communities of the coastal plain
Upland (Inland)	Mesic mixed hardwood forest	Terrestrial system	Low elevation mesic forests
Upland (Coastal)	Maritime shrub	Terrestrial system	Communities of the coastal zone
	Maritime evergeen forest	Terrestrial system	Communities of the coastal zone
	Maritime deciduous forest	Terrestrial system	Communities of the coastal zone
	Salt shrub	Esturaine system	N/A
Marshes/ Nonforested Wetlands	Dune grass	Terrestrial system	Communities of the coastal zone
	Maritime dry grassland	Terrestrial system	Communities of the coastal zone
	Maritime wet grassland	Palustrine system	Nontidal coastal fringe wetlands
	Interdune pond	Palustrine system	Nontidal coastal fringe wetlands
	Tidal freshwater marsh	Palustrine system	Freshwater tidal wetlands
	Salt marsh	Esturaine system	N/A
	Brackish marsh	Esturaine system	N/A
	Salt flat	Esturaine system	N/A
	Upper beach	Marine system	N/A
Swamps	Nonriverine wet hardwood forest		
	Nonriverine swamp forest		
	Natural lake shoreline	Palustrine system	Coastal plain depressions and water bodies
	Maritime swamp forest	Palustrine system	Nontidal coastal fringe wetlands
	Maritime shrub swamp	Palustrine system	Nontidal coastal fringe wetlands
	Esturine fringe loblolly pine forest	Palustrine system	Nontidal coastal fringe wetlands
	Tidal cypress–gum swamp	Palustrine system	Freshwater tidal wetlands

are the focus of considerable study and conservation action (Odum et al. 1984, Benoit and Askins 2002, Kushlan et al. 2002, Street et al. 2004). Nonetheless, based on field observations in this study, these habitats support almost no lichen diversity, and thus were not

inventoried (Lendemer and Harris, pers. obs.). This paucity of lichens in nonforested wetlands is due to the absence of suitable substrates, namely rocks, robust woody vegetation, and organic matter not submerged by saltwater.

Table 2. Summary of lichen diversity across Dare Regional Biodiversity Hotspot (DRBH) habitat types as well as the pairwise similarities of their overall lichen communities.

	% of DRBH		Sørensen Similarity				
	Taxonomic Diversity	Taxonomic Diversity	Swamp Forests	Pocosin Peatlands	Atlantic White Cedar Peatlands	Maritime Forest Uplands	Inland Uplands
Swamp Forests	314	83	—	—			
Pocosin Peatlands	69	18	0.35	—			
Atlantic White Cedar Peatlands	89	23	0.387	0.443	—		
Maritime Forest Uplands	207	54	0.599	0.341	0.345	—	
Inland Uplands	77	20	0.379	0.438	0.301	0.401	—

Of the three types of forested habitats in the DRBH, the region is dominated by low-lying forested wetlands and slightly elevated peatlands. In fact, within the two largest protected areas of the DRBH, Alligator River and Pocosin Lakes National Wildlife Refuges, more than 232 km² and 615 km² of land fall into these groups, respectively (US Department of the Interior 2007, 2008). The taxonomic diversity of lichens found in forested wetlands, peatlands and uplands is summarized and compared in Table 2.

By far, peatlands comprise the largest natural communities in the DRBH in terms of total land area, and these are dominated by different types of pocosins (see Figure 2 for examples). Due to the dense vegetation and frequent deep canals surrounding them, pocosins are difficult to access, let alone inventory. During our work in the MACP, we found only one species that appeared to be restricted to pocosins, a new species of *Megalaria* described herein, which was found twice at one site in Alligator River National Wildlife Refuge. Otherwise, the lichen communities of pocosins are composed of species that are widespread in adjacent swamp forests where understories host low lichen diversity, because they are extremely shaded. Nonetheless, future studies of pocosins, particularly focusing on the upper boles and canopy, could reveal additional specialized taxa not collected during our inventory.

The nonpocosin peatlands in the DRBH are composed of Atlantic white cedar (*Chamaecyparis thyoides* (L.) Britton) forests (Figure 3A). Atlantic white cedar typically forms dense, even-aged stands and is dependent on specific conditions for regeneration (Laderman 1989). The species has been extensively logged in the past, and the peatlands it forms ditched and

drained, such that the ecosystem is now considered globally threatened (Laderman 1989, Burke and Sheridan 2005). Our inventory of Atlantic white cedar peatlands in the DRBH was limited primarily because only a small number of stands were deemed suitable for inventory. The majority of candidate sites were ruled out based on field observations that they hosted few if any lichens, owing to young stand age wherein tree stems were densely crowded and small. Furthermore, many of the remaining stands were impossible to access without specialized equipment or logistical support. We did inventory one pure Atlantic white cedar stand, as well as several stands where the species was present as a minor component of the forest. Our inventory largely confirmed prior studies of Atlantic white cedar peatlands (Torrey 1933, Thomson 1935, Little 1951, Brodo 1968, Harris 1985, Lendemer 2006; Lendemer unpubl. data from Delmarva and New Jersey) that have found that, although the habitat has a distinctive community of lichens, the same species also occur in swamp forests on other coniferous hosts, particularly cypress and pine. This phenomenon is illustrated by species such as *Chrysothrix chamaecyparicola* and *Micarea chlorosticta*, which often dominate corticolous Atlantic white cedar communities in North Carolina and elsewhere, but also occur less frequently and less abundantly on cypress and pine in other swamp forests (Lendemer and Elix 2010; Lendemer, unpubl. data).

The most diverse lichen communities in the DRBH occur in the swamp forests, which, unlike peatlands, usually have relatively widely spaced trees and comparatively open understories (Figures 3B–3D; Kellison and Young 1997, Lorber and Rose 2015). Presumably, the abundance of diverse microhabitats stemming from more

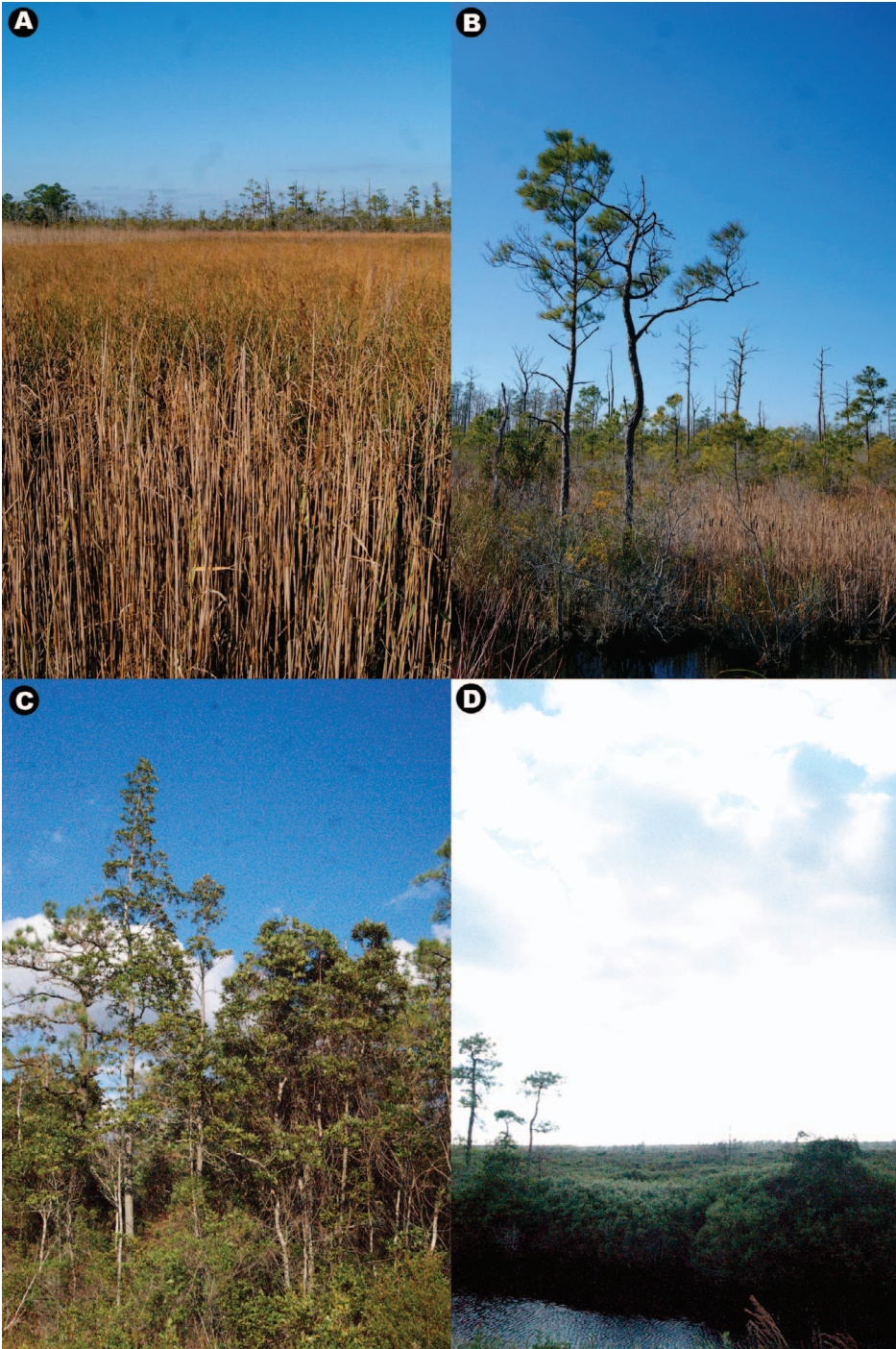


Figure 2. Pocosin habitats in the Dare Regional Biodiversity Hotspot (all from Dare County). A. Marshland grading to pond pine (*Pinus serotina*)–shrub pocosin. B. Pond pine–shrub pocosin. C. Pond pine–cane (*Arundinaria*) pocosin with loblolly bay (*Gordonia lasianthus*). D. High shrub pocosin dominated by shrubs and *Smilax* with sparse pond pine.



Figure 3. Swamp forest habitats in the Dare Regional Biodiversity Hotspot. A. Atlantic white cedar (*Chamaecyparis thyoides*) swamp in Dare County. B. Bald cypress (*Taxodium distichum*) swamp in Tyrrell County. C. Tupelo (*Nyssa*) swamp in Dare County. D. Red maple (*Acer rubrum*) –dominated mixed hardwood swamp in Tyrrell County.

extreme light and humidity gradients, regularly fluctuating water levels, and higher diversity of hosts (i.e., many different hardwoods and conifers, often in varying composition) are factors that have fostered rich and diverse lichen communities in the swamp forests of the DRBH. However, it is significant that the DRBH also includes some of the largest and most intact stands of mature swamp forests that we encountered in the MACP (see, e.g., Sorrie 2014a, Lorber and Rose 2015). The low degree of past disturbance and larger contiguous forested areas relative to other parts of the MACP may also have facilitated the survival of lichens in the DRBH that were once more common and widespread in the Coastal Plain. This is evidenced by the finding that the DRBH, and specifically mature swamp forests, host the highest cyanolichen diversity of any sites we inventoried in the MACP, including species that we did not encounter elsewhere, such as *Parmeliella pannosa* (Sw.) Müll. Arg. and *Pannaria tavaresii* P.M. Jørg. (Lendemer and Goffinet 2015). Furthermore, the area with the richest cyanolichen communities in the DRBH is also where we discovered a new species of the macrolichen genus *Sticta*, *S. deyana* Lendemer & Goffinet (see Lendemer and Goffinet 2015). That species is locally common in a small area of Alligator River National Wildlife Refuge, but otherwise known from a single mature hardwood forest in Alabama. *Sticta* is an easily recognized and conspicuous genus, and the distribution of *S. deyana* almost certainly reflects actual rarity, rather than a lack of adequate lichen exploration in southeastern North America.

Uplands in the DRBH fall into two categories: protected maritime forests on barrier islands (Figures 4B–4D) and small isolated inland “islands” of upland surrounded by swamp forests (Figure 4A). Historically, there would have been large areas of upland forests on the inner portions of the DRBH mainland; however, these have been almost entirely converted for silviculture, agriculture, and other uses (Dey et al. 2010, Noss et al. 2015). The small number of remaining upland forest sites, most of which are confined to barrier islands, limited our ability to inventory upland forests as extensively as the much larger and more intact swamp forests. Even the remaining upland forests on barrier islands have been severely fragmented and

degraded (Lopazanski 1987, Bellis 1995, Berman and Berquist 2007). Nonetheless, maritime forests were the second most diverse habitat inventoried, with 207 taxa or 54% of the total known from the DRBH. Although these habitats share many species with inland swamp forests, they also have a distinct group of species that does not occur on the mainland, and even includes narrow endemics, such as *Phaeographis oricola* Lendemer & R.C. Harris (Lendemer and Harris 2014a, Lendemer and Harris 2015).

Although we inventoried only one inland upland forest in the DRBH, that site hosted 20% (77 taxa) of the total DRBH diversity, and was unlike all other sites that we inventoried. The site consisted of a narrow upland ridge surrounded by a mixed hardwood swamp populated with relatively mature beech (*Fagus grandifolia* Ehrh.) forest. The recently described species *Acanthothecis paucispora* Lendemer & R.C. Harris was located at this site, and remains known from only two strongly disjunct locations that are both in the MACP (Lendemer and Harris 2014a). A crustose lichen that produces conspicuous pycnidia and apothecia, with polysporous asci containing numerous globose ascospores, was also found at this site. This taxon was not found elsewhere in the DRBH, and is so unlike any other of which we are aware that it is described herein as a new genus and species (*A. pamlicoensis*). The number of rare and unusual species found at the one inland upland site that we inventoried highlights an important avenue for future study, and hints at the richness that lichen communities in upland hardwood forests once attained in the region.

Taxonomic Diversity

Taxonomic diversity (i.e., the number of species and infraspecific taxa) found at each site is summarized in Figure 5. Although taxonomic diversity values vary greatly across the DRBH (min. = 24, max. = 150), the average diversity was high ($\bar{x} \pm s = 67 \pm 23$) compared to other regions of the MACP (Lendemer and Allen 2014), with 57% ($n = 24$) of the sites hosting ≥ 80 taxa. Similarly, although collection effort was held constant across sites, the number of vouchers collected varied greatly (min. = 30, max. = 322), with an average of 100 ± 48 vouchers collected at each site. There is also a strong positive correlation between the number of collections and taxonomic diversity (Figure 6; $R^2 = 0.9149$),

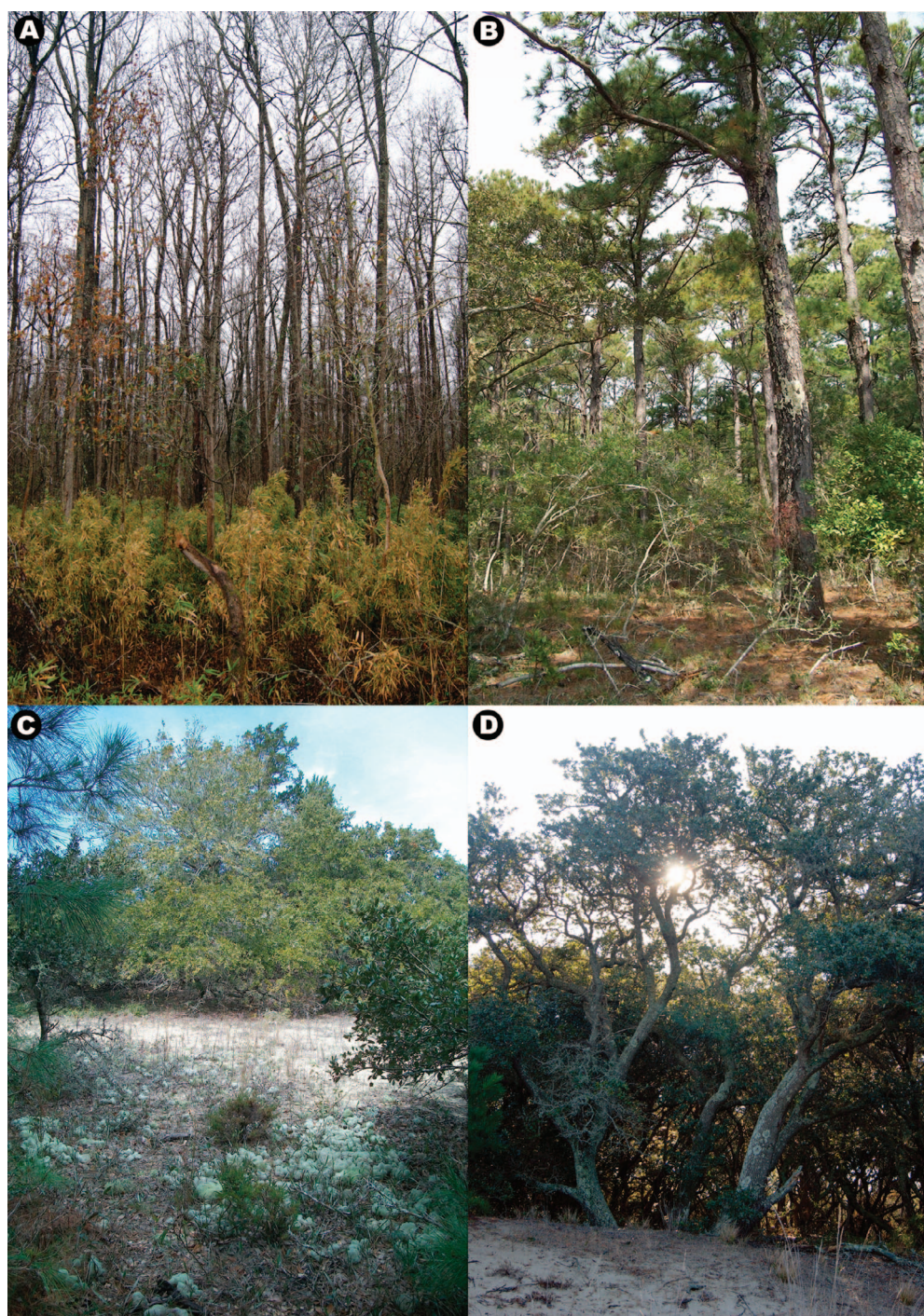


Figure 4. Upland habitats in the Dare Regional Biodiversity Hotspot. A. Mixed hardwood forest dominated by oaks (*Quercus*) and maple (*Acer*) with dense understory of cane (*Arundinaria*), Tyrrell County. B. Maritime forest dominated by loblolly pine (*Pinus taeda*) with an understory of mixed shrubs dominated by yaupon (*Ilex vomitoria*), Dare County. C. Stabilized dune scrub dominated by lichen ground cover (*Cladonia evansii*, *C. leporina*, *C. subtenuis*) and live oaks (*Quercus virginiana*), Dare County. D. Maritime forest dominated by live oak, Currituck County.

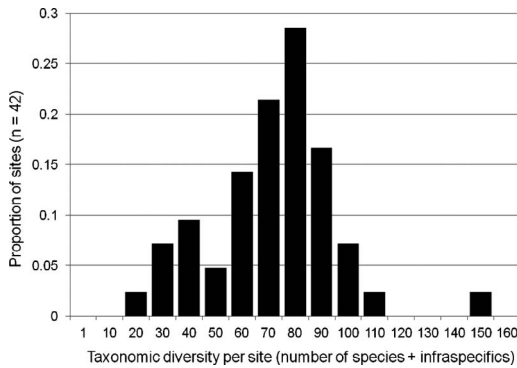


Figure 5. Graph summarizing taxonomic diversity at each site across the Dare Regional Biodiversity Hotspot.

which suggests that the team inventories conducted for this study did not result in repeated collection of the same species at the same sites, either by the same individual or between individuals. Of the 386 taxa encountered during the inventory, 97% ($n = 360$) were identifiable to species or infraspecific taxon, with the majority of the remaining 3% ($n = 10$) identified to genus and likely representing additional undescribed species.

Species Traits

Given the sampling strategy and large number of samples, we were curious to understand the frequencies of lichen traits in the study area. As such, we examined three commonly analyzed lichen traits (growth form, photobiont, and reproductive mode) as they relate to taxonomic diversity, the total number of specimens examined, and the total pooled occurrences for all species. Although limited, the examination of quantified traits performed for this study yielded a number of interesting results, which are summarized in Table 3.

From the standpoint of growth form, the DRBH lichen biota is dominated by crustose lichens, which comprise fully 71% (272 taxa) of total lichen taxonomic diversity. Although intuitive, given the widely recognized diversity of crustose lichens, it is nonetheless surprising that the much more conspicuous and well-studied macrolichens comprise less than one-third (30%: 21% foliose lichens, 9% fruticose lichens) of the diversity. A similarly interesting result is that 68% (258 taxa) of the species in the DRBH reproduce sexually (i.e., produce apothecia or perithecia, and are presumed not to reproduce

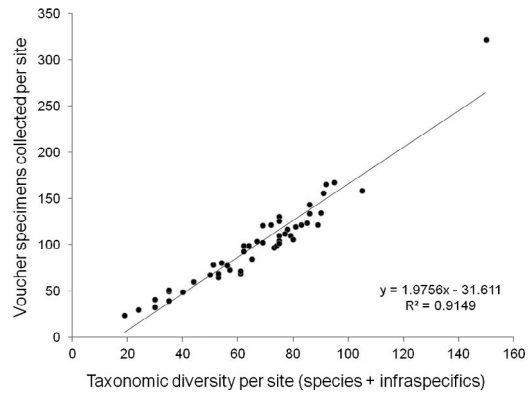


Figure 6. Scatter plot comparing collection effort (the number of collections made at each site) to taxonomic diversity on a per-site basis. Note that the outlier status of the highest diversity site may be due to the fact that it was the only site visited twice, once by the original inventory team, and then again by the participants of the Tuckerman Workshop.

primarily through vegetative means), while 30% (113 taxa) reproduce through the dispersal of lichenized diaspores. The results for photobiont type are not unexpected for a temperate region with subtropical elements, as more than half (55%, 212 taxa) have a coccoid green algal photobiont and nearly a third (28%, 108 taxa) have *Trentepohlia* as a photobiont. The latter is a photobiont that is much more frequent in humid tropical regions compared to temperate or arctic regions (Nash et al. 1987, Matos et al. 2015). It is also noteworthy that small percentages of the species in the DRBH lack a photobiont (4%), are lichenicolous on other lichens (9%), or have a cyanobacterial photobiont (4%). Although the small number of cyanolichens present in the region may reflect a natural pattern, it is also possible that the number reflects declines as a result of habitat degradation and pollution (discussed in the “Overview: Vegetation and Lichen Diversity” section above). Finally, it is significant that the overall frequencies of different trait states in our diversity data were similar to those for the same trait states summarized from the numbers of vouchers and occurrences of each taxon. This suggests that our sampling was not biased toward any one trait state (i.e., the percentage of vouchers is negligibly different from the percentage of taxonomic diversity) and that the occurrence of a given trait state across the studied sites was

Table 3. Summary of Dare Regional Biodiversity Hotspot taxonomic diversity and voucher/occurrence numbers, broken down by three commonly used lichen traits. Note that totals do not match voucher totals reported elsewhere herein, because they do not include unidentified specimens/taxa.

	This Study					
	Species		Vouchers		Occurrences	
	N	%	N	%	N	%
Growth Form						
Crustose	272	71	3,263	68	2,128	67
Foliose	80	21	1,292	27	887	28
Fruticose	34	9	248	5	187	6
Total	386		4,803		3,202	
Photobiont						
Cyanobacteria	17	4	94	2	79	2
Lichenicolous	34	9	137	3	108	3
Other Green Algae	212	55	3,238	68	2,161	68
Photobiont absent	15	4	30	1	27	1
Trentepohlia	108	28	1,304	27	827	26
Total	386		4,803		3,202	
Reproductive Mode						
Fungal Asexual	15	4	73	2	59	2
Lichenized Asexual	113	30	1,840	38	1,233	39
Sexual	258	68	2,890	60	1,910	60
Total	386		4,803		3,202	

negligibly different from the percentage of taxa with that trait state.

It should be noted that a logical extension of this aspect of our study would be to examine functional diversity, as well as trait distributions and correlates. We refrained from undertaking these analyses, because our dataset is taken from a relatively small geographic area. Instead, we will perform them on a much larger dataset covering the full MACP in a forthcoming study. It will be particularly interesting to see if the proportions of fruticose, asexual, cyanobacterial, or *Trentepohlia*-associated species observed in the DRBH are higher than in less intact and more degraded areas of the MACP. This is because previous studies of other regions have positively correlated numbers (diversity, frequency, and abundance) of taxa with those traits to higher-quality intact habitats (Marini et al. 2011, Stofer et al. 2006).

Comparison with Existing Data

It has already been highlighted above that one of the primary reasons for undertaking our inventory of the MACP, and by extension the DRBH, was that the region had previously been poorly studied. This is evidenced by the small number of floristic and taxonomic treatments that have covered the area, and by the fact that only 68 collections were documented from the DRBH in

CNALH as part of the large-scale efforts to digitize lichen herbaria in the USA (see data deposited in Dryad). The majority of these were concentrated in highly visited areas of coastal barrier islands (Figure 1C). Although we acknowledge that there are almost certainly undigitized vouchers from the DRBH in other herbaria, there is no doubt that the collection bias and small number of vouchers reflect actual data gaps rather than data resource artifacts. With the substantial disparities between the pre- and poststudy data in mind, we nonetheless attempted to determine what impacts result from drawing conclusions from the prestudy data alone. This is salient, because large amounts of digitized lichen specimen data are now easily accessible online, and such data are actively being used without clear acknowledgement of their limitations.

First, we summarized and examined the CNALH raw data for DRBH lichens. Of the 68 vouchers that were available, 8 were undetermined and 24% (18 vouchers) were identified as 16 taxa that we did not encounter in our inventory. These are almost certainly misidentified, since available data indicate that the species do not occur within, or in some cases even near, the DRBH or the MACP (e.g., *Lecanora albellula* (Nyl.) Th. Fr. is so far unknown from eastern North America, *Lep-*

aria caesiella R.C. Harris does not occur south of the Delmarva Peninsula in the Coastal Plain, *Parmotrema perlatum* (Huds.) M. Choisy occurs much further inland, and all MACP specimens we have seen that are morphologically assignable to *P. subtinctorium* (Zahlbr.) Hale are actually *P. neotropicum* Kurok.). It is also likely that nomenclature updates of historical identifications resulted in several of these errors. For example: (a) *Cladonia subcariosa* Nyl. is broadly applied to a group including what we recognize as *C. polycarpia* G. Merr.; (b) *Ramalina fastigiata* (Pers.) Ach. would be updated to *R. americana* Hale, but that species is not known to occur in the DRBH; and (c) *Bacidia atrogrisea* (Delise) Körb. is a synonym of *B. laurocerasi* (Delise ex Duby) Zahlbr., but that species does not occur in the Coastal Plain. It is also possible that some of the vouchers are correctly identified. For instance, a voucher of *Pseudocyphellaria crocata* (L.) Vain could very well represent a collection of a species that is now extirpated from the DRBH. The above issues could be resolved by a loan of specimens from the relevant institution, and we assert that, before including CNALH data in lichen biodiversity assessments, any suspect specimens should be verified by physical examination. It should also be noted that, while we have opted not to examine these collections for this study, we did revise and examine all of the existing prestudy vouchers at NY, which were greater in number than those available in CNALH.

After summarizing the available data for the DRBH from CNALH, it was clear that sampling was strongly biased toward the coast, and the most diverse areas found in our study had not previously been sampled. Thus, any lichen threat assessment based on these data would have prioritized conservation efforts on the coastal barrier islands, which indeed are highly threatened, but ignored inland swamps that are similarly imperiled by sea-level rise, but host higher levels of diversity.

Lichen Community Similarity

Pairwise comparisons of the species compositions of the 49 sites inventoried for this study revealed a low degree of similarity between sites (Sørensen $\bar{x}$ = 0.35 ± 0.12), suggesting a high degree of heterogeneity among sites. Indeed, the similarity values for sites in the DRBH are much lower than

those obtained from a study on the nearby Delmarva Peninsula (Ray et al. 2015), a subregion of the MACP that hosts lower lichen diversity and has highly fragmented natural habitats (Lendemer and Allen 2014). A summary of taxonomic diversity and community similarity between the habitat types discussed in the “Overview: Vegetation and Lichen Diversity” section (above) is presented in Table 2. Overall, similarity between the lichen communities of different habitat types was low. Swamp forests and maritime forest uplands, on the other hand, were ~60% similar. This relatively higher degree of similarity is likely to be due to isolated swamp forests occurring within maritime forests on barrier islands (see “Distribution Patterns” below).

A high degree of lichen community heterogeneity is further supported by examination of the number of vouchers and number of occurrences per taxon, which are summarized in Figure 7. Remarkably, 23% ($n = 88$) of the taxa were collected only once, and fully 67% ($n = 249$) were collected 10 or fewer times (this includes multiple collection events at a single site). Thus, only 33% ($n = 133$) of the 386 taxa found in this study were collected more than 10 times, with 16% or 58 taxa which were collected between 11 and 20 times accounting for 77% of the taxa collected more than 10 times. The results of the occurrence data present a similar picture, with 27% ($n = 100$) taxa located at only 1 site, 74% ($n = 275$) taxa located at 10 or fewer sites, and only 29% ($n = 107$) taxa located at more than 10 sites. Again, regardless of whether one examines the total number of vouchers collected per taxon or the number of sites at which a given taxon occurred, more than half of the taxa were encountered only a small number of times, and a surprising number were collected or located only once.

Overlap between Collectors

Given that this was a study wherein a team of multiple experts inventoried sites of approximately equal size and with approximately equal effort, we examined a subset of the study sites to determine the amount of overlap between the species assemblages collected by different members of a team at a given site. Pairwise comparisons of the species assemblages collected by 3 team members (J.L.C., R.C.H., and W.R. Buck) at 24 sites revealed levels of similarity below 50% (Table 4). This supports anecdotal information and smaller studies (see Lendemer et al. 2013), suggesting that even within the small area

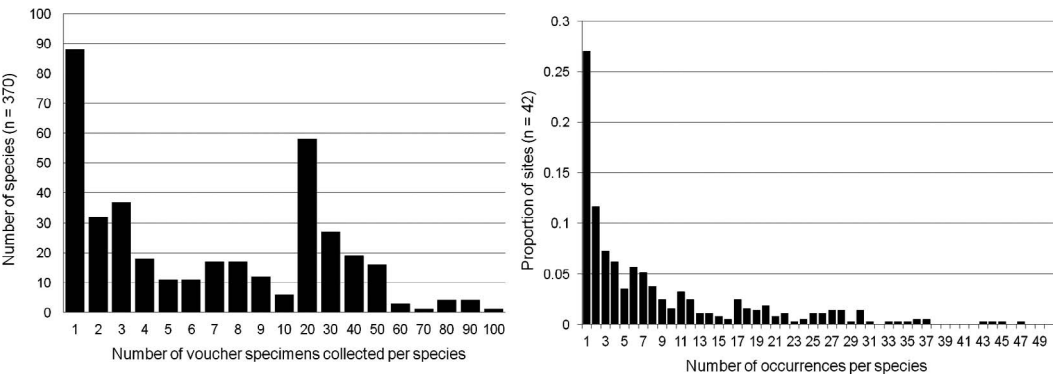


Figure 7. Graphs summarizing the number of vouchers (left) and number occurrences (right) for species in the Dare Regional Biodiversity Hotspot.

reasonably surveyed for less than an hour, individuals will still collect very different assemblages of species. This is likely attributable to a combination of several factors, namely: (a) individually specific search patterns wherein one person may focus on the boles of trees, while another may focus on branches, roots, humus, or rocks; (b) individually specific taxonomic focuses (e.g., calicioid fungi, macrolichens, pyrenolichens, sterile lichens) that manifest even when conducting a complete biodiversity inventory; and (c) the actual existence of many more species in a small area than has generally been appreciated previously. Although the overlap between collectors may be greater in areas that host low levels of biodiversity, our results in particular highlight the importance of relying on trained experts to conduct biodiversity assessments and inventories. Results also highlight the value of a team approach, when the goal is to document total biodiversity. Indeed lichens are a nonmonophyletic group comprising species that belong to multiple fungal lineages. The expectation that a single individual will recognize and capture all lichen biodiversity is akin to expecting one mycologist to inventory all fungi or one biologist to document all invertebrate life.

Distribution Patterns

Examination of the distributions of 337 species within the DRBH and adjacent areas of the MACP (i.e., including the Chowan River Drainage and Great Dismal Swamp to the north, and Carteret County, Croatan National Forest, and the Pamlico Peninsula to the south) revealed distinct patterns and trends. The table summa-

rizing species distributions, and the maps used in this part of this study, are both included in the data archive submitted to Dryad.

From the standpoint of overall distributions within the DRBH and adjacent areas of the MACP, assemblages of species were found to occur only in either inland swamp habitats or coastal maritime forests. These patterns reflect major differences in environmental conditions and vegetation (Schafale and Weakley 1990, Bellis 1995), and, although well documented in vascular plants (Kearney 1901, Bordeau and Oosting 1959, Griffith et al. 2002, Fleming 2012), they have been little studied in lichens. The phenomenon is illustrated by the genus *Haematomma*, wherein four species (*H. accolens*, *H. americanum*, *H. flexuosum*, and *H. guyanense*) occur only at inland sites, while one species is restricted to only maritime sites (*H. persoonii*). Of the taxa mapped for this study, 136 (41%) were found only at inland sites, 26 (8%) were found only in maritime sites, and 175 (52%) were found at both kinds of sites. Although 36 (11%) of the taxa were represented by only 1 occurrence on the distribution map,

Table 4. Overlap between species assemblages collected by three team members at 24 sites in the Dare Regional Biodiversity Hotspot expressed as the average $\pm$ SD of Sørensen similarity values obtained from all possible pairwise comparisons (n = 24 comparisons per collector pair).

	Buck	Harris	Lendemmer
Buck	—		
Harris	0.180 $\pm$ 0.093	—	
Lendemmer	0.170 $\pm$ 0.087	0.318 $\pm$ 0.093	—

these singletons were disproportionately inland (29 taxa, 81% of singletons), while only a small number were maritime (4 taxa, 11% of singletons).

The large number of taxa found at both inland and maritime sites must also be interpreted in light of two factors. First, while some taxa are truly restricted to maritime habitats throughout their ranges in North America (Moore 1968, Harris 1995; Lendemer and Harris 2014a, 2015), many species are distributed only in such habitats at the northern edge of their range (e.g., Delmarva to South Carolina) and then also occur inland once they reach Florida (Brodo et al. 2008, Lendemer and Harris 2014b). Second, many of the taxa scored as present in both inland and maritime sites were mostly restricted to one region, with only one to several occurrences in the other region. Such outlier occurrences were of two types: (a) inland taxa present in mature deciduous maritime forests that occur on the inland sides of barrier islands (e.g., the majority of such singleton maritime occurrences of inland species are from an unusual hardwood forest at Kitty Hawk NERR); or (b) maritime taxa present in groups at a small number of unusual inland sites (e.g., the inland occurrences of *Dirinaria confusa* and *Xyleborus nigricans*). It is interesting to note that, although inland and maritime sites clearly host unique assemblages of taxa, these two groups of sites are less similar to each other (Sørensen $\bar{x} \pm s = 0.26 \pm 0.09$ between inland and maritime sites) when compared to the similarity among sites within each group (Sørensen $\bar{x} \pm s = 0.41 \pm 0.11$ for inland sites, 0.35 ± 0.11 for maritime sites).

In addition to the differences between inland and maritime habitats, an interesting pattern was noted, wherein some lichenicolous fungi were found only at inland sites, while their hosts were widely distributed throughout the study area (Figure 8). An example of this pattern is *Gyalideopsis floridae*, which is lichenicolous on members of the genus *Parmotrema*, particularly *P. submarginale* and *P. subrigidum*, both of which were widely distributed in the DRBH. In many cases, however, the distribution of the lichenicolous fungus does mirror that of the host, such as *Buelliella tryptethelii* which was found only at inland sites where its host *Bathelium carolinianum* occurred, and *Vouauxiella lichenicola*, which occurs on different crustose lichens, but in the Coastal Plain is

most common on *Lecanora louisianae* and found wherever that species occurs.

Floristic Elements

The Mid-Atlantic region of the Atlantic Coastal Plain is a biological transition zone that includes boreal or northern temperate and southern subtropical or tropical floristic elements in varying proportions, largely depending on latitude (Kearney 1901, Transeau 1903, Torrey 1937, Beaven and Oosting 1939, Ahti 1961, Dirig 1990, Lendemer and Knapp 2007). The DRBH fits well within this pattern, as evidenced by the taxa with continuous distributions in the Coastal Plain that have their northern limit (76 taxa, 21%) or southern limit (9 taxa, 3%) in the region. The large number of species with northern distributional limits in the DRBH supports the characterization of the region as hosting a biota dominated by southern or subtropical elements. Examples of taxa at the northern limits of their geographic ranges include members of genera that are particularly diverse in subtropical and tropical regions, such as *Bactrospora* (*B. brevispora*, *B. carolinensis*, *B. lamprospora*), *Dirinaria* (*D. aegialita*, *D. confusa*, *D. picta*), *Fissurina* (*F. alligatorensis*, *F. columbina*, *F. incrustans*, *F. illiterata*, *F. scolecitis*), *Ocellularia* s.l. (*O. americana*, *O. praestans*, *O. sanfordiana*), and *Pyrenula* (*P. anomala*, *P. cruenta*, *P. microcarpa*, *P. microtheca*, *P. santensis*). The northern distributional limit of foliicolous lichens in the Coastal Plain is also located in the DRBH. *Asterothyrium decipiens* occurs as sterile or pycnidiate thalli on the leaves of *Persea* Mill. in inland swamps, and *Fellhanera bouteillei* occurs as pycnidiate thalli on fronds of *Sabal minor* (Jacq.) Pers. in maritime forests. The populations of *S. minor* in the DRBH also represent the northern distributional limit of that species, and of the entire palm family (Arecaceae) in eastern North America (Tripp and Dexter 2006). It is interesting to note that both of the foliicolous lichens that are at the northern edge of their range in the DRBH only occur as sterile thalli with pycnidia.

Examples of taxa at the southern limits of their geographic ranges in the Coastal Plain include such northern temperate species as *Anzia colpodes*, *Arthonia ruana*, *Flavoparmelia caperata*, *Lepraria harrisiana*, *Micarea peliocarpa*, *Phaeocalicium polyporaenum*, and *Ropalospora viridis*. Many of the 230 taxa (66%) found in the DRBH that occur both north and

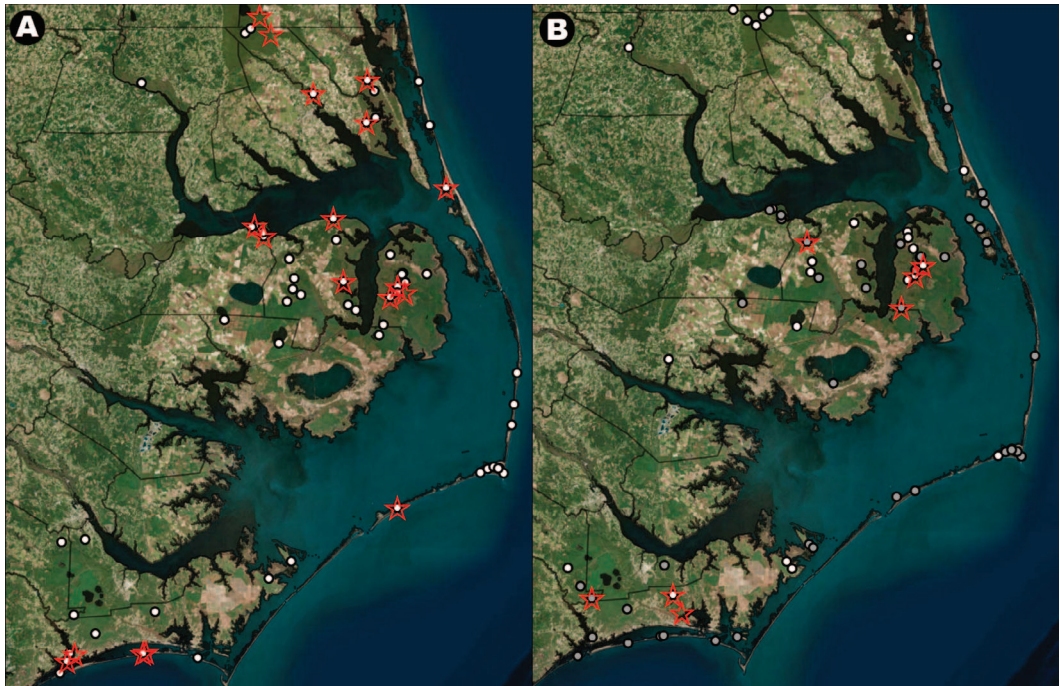


Figure 8. Comparison of lichenicolous fungus distributions between two hosts that occur throughout the Dare Regional Biodiversity Hotspot. A. *Vouauxiella lichenicola* (stars) occurs at both inland and maritime sites on *Lecanora louisianae* B. de Lesd. B. *Gyalideopsis floridae* (stars) occurs only at inland sites, although the hosts, *Parmotrema perforatum* (white circles) and *P. submarginale* (gray circles), occur at both inland and maritime sites.

south of the region are near the northern or southern limits of their geographic ranges within the Coastal Plain (Lendemer, unpubl. data). Since the only significant barriers for north–south lichen migration within the Coastal Plain are water bodies and availability of suitable habitat, the latter being a geologically recent anthropogenic constraint (Napton et al. 2010, Terando et al. 2014), understanding the present-day distributional limits of species establishes an important benchmark for future studies of global environmental change.

In addition to the temperate and subtropical elements present in the DRBH, there are two floristic elements that merit comment, one comprised of taxa endemic to the Coastal Plain of southeastern North America, and another comprised of tropical taxa that are disjunct from their ranges much further south in the Coastal Plain. The disjunct occurrence of subtropical and tropical species in the DRBH is not surprising, given that the region is characterized by a more southern lichen biota. Nonetheless, the majority of subtropical and

tropical species found in the DRBH have been shown by our work elsewhere in the MACP to have continuous distributions in the Coastal Plain south of the DRBH (e.g., Lendemer and Harris 2015). Thus, taxa that are truly disjunct between the DRBH and the nearest populations often located >500 km to the south, such as *Acrocordia gemmata*, *Bactrospora brevispora*, *Parmeliella pannosa*, and *Pyrgillus javanicus*, are exceptions.

Endemic plants and animals have long been recognized as occurring both in the Coastal Plain and in its many subregions (e.g., Sorrie and Weakley 2001, Fleming 2012). In the MACP, the most iconic example may be the venus flytrap (*Dionaea muscipula* J. Ellis), narrowly endemic to a small portion of North Carolina and South Carolina (Sorrie and Weakley 2001). Lichens are no exception to this pattern of endemism, and while many species that occur in the Coastal Plain also occur in other tropical regions of the world, there are also many endemics and near endemics from a wide range of macrolichen and microlichen groups (Brodo 1968, Moore 1968,

Harris 1995, Lücking et al. 2011, Lendemer and Harris 2015). Only two species discovered in our inventory appear to be endemic to the DRBH, *A. pamlicoensis* from Bull Neck Swamp and *Lichenochora haematommatus* parasitic on *H. persoonii* from Hatteras Island. Otherwise, no other species are strictly endemic to the DRBH, although many are nearly endemic to the region. Examples of such taxa include *Sticta deyana*, which occurs in mature inland swamp forests, and *Phaeographis oricola*, which occurs in mature maritime forests on barrier islands.

Threats to the Lichen Biota

The remaining natural habitats in the MACP, and specifically in the DRBH, have been classified as threatened or endangered (e.g., Kirby-Smith and Barber 1979, Bellis 1995, Riggs and Ames 2003, Brown et al. 2005, Berman and Berquist 2007, Sallenger et al. 2012, Lorber and Rose 2015, Noss et al. 2015, US Army Corps of Engineers 2015). However, these assessments have not taken into account lichen diversity, an important and conspicuous component of the vegetation (see Lendemer and Allen 2014). The threats to DRBH lichen communities can be divided into two groups: those that have already had impacts in the past and will continue into the immediate future, and those that are projected to materialize in the future.

It is clear that the most significant impacts to the inland DRBH lichen communities have resulted from large-scale conversion of natural habitats for human uses (agriculture, silviculture) as well as from resource extraction (e.g., Lorber and Rose 2015). Although the initial loss of suitable lichen habitat and substrates from these activities was immediate and substantial, long-term impacts of large-scale ditching and draining of water-logged swamps and peatlands have been far more pervasive and persistent, because hydrological regimes have been altered (Phipps et al. 1978, Kirby-Smith and Barber 1979, Daniel 1981, Ash et al. 1983). In the DRBH, like many areas of the MACP, natural habitats that remain primarily have poor soils unsuitable for agriculture (e.g., the sandhills), lie in difficult-to-access floodplains (e.g., bottomland swamps along rivers), or have persisted despite repeated attempts to alter them for human uses (e.g., swamps and peatlands). The scale and degree of changes associated with historical ditching and draining is difficult to appreciate in the present time. To place these effects in context, consider

that attempts to drain the Great Dismal Swamp on the border of North Carolina and Virginia were initiated by George Washington in the late 1700s so that the 45,000-ha swamp that remains today is less than a third of its original area (see, e.g., Morse 1804, Kearney 1901, Simpson 1998). Although the importance of wetlands, swamps, and natural habitats generally has gained increasing recognition (Noe and Hupp 2005, 2009), the DRBH, like many other regions of the eastern USA continues to be affected by irreversible losses of habitat due to development and degradation of habitats by diverse forces (e.g., Figures 9A, 9C).

While the impacts of anthropogenic land use have been substantial and continue to persist as ongoing threats to biodiversity, the potential loss or irrevocable alteration of large areas through global climate change and sea level rise are major long-term issues for the DRBH (Riggs and Ames 2003, Sallenger et al. 2012). Much of the DRBH, including the lowest-lying swamp forests that host the highest lichen diversity in the MACP, is well within 1.5 m of current sea level, and is projected to be inundated by 2100 under the most conservative estimates (Figures 9B, 9D; Lendemer and Allen 2014). Although large areas of these unique habitats have been protected for the present, their continued existence into the future remains far from certain.

Conservation

Although many of the natural communities in the DRBH cover large spatial areas, in some cases these are among the largest and best-preserved examples of those communities remaining (e.g., Lorber and Rose 2015). Furthermore, several of these communities are treated as critically imperiled, endangered, or rare within North Carolina and at a global scale (US Department of the Interior 2007, 2008). Thus, at both the natural community level and even landscape scale, the DRBH includes substantial protected areas that are vital to maintaining the integrity of the Atlantic Coastal Plain biome and the ecosystems services it provides.

In this context, the DRBH serves as the primary lichen biodiversity reservoir for the MACP (Lendemer and Allen 2014). Indeed, the region hosts the core ranges and largest populations of endemic, near-endemic, and regionally or globally rare or threatened species. As such, the DRBH lichen communities function as crucial, and in some cases the only, diaspora



Figure 9. Examples of threats to the Dare Regional Biodiversity Hotspot lichen biota and habitats. A. Clear-cut logging of hardwood swamp parcel (cut 2014, inventory of adjacent protected area completed in 2013). B. Erosion of the shoreline. C. Development, construction, and maintenance of infrastructure, including highways and bridges. D. Sea-level rise, as exemplified by the conversion of healthy pocosins and swamp forests to marsh and, eventually, open water.

banks with which to establish new populations or attempt translocations. Research on the conservation and management of these source populations, as well as development of mitigation strategies to facilitate migration inland at pace with sea level rise, are an immediate concern and should be prioritized. This is particularly the case when one considers that, even under conservative estimates, sea level rise-related impacts to the DRBH are projected to be disproportionate compared to the rest of the MACP, and to occur within a relatively short time frame (Riggs and Ames 2003, Sallenger et al. 2012).

CONCLUSION That the lichens of both the MACP and the DRBH, two regions visited by millions of tourists annually and within several hours drive of major metropolitan areas, have received so little study previously, is remarkable. The data and results presented here not only provide the first comprehensive account of lichen biodiversity in the DRBH, but indeed for any large region of the Coastal Plain in southeastern North America, a biodiversity hotspot long known to host unique and diverse communities of plants and animals (James 1961, Estill and Cruzan 2001, Sorrie and Weakley 2001, Noss 2013, Noss et al. 2015). While a small number of accounts of southeastern Coastal Plain lichen biodiversity have been published, these have covered smaller areas with less-intensive sampling efforts (e.g., Hodgkinson and Case 2008, Lücking et al. 2011) or been taxonomically incomplete (e.g., Moore 1968, Harris 1995).

The present study also summarizes diversity of an important component of obligate symbiotic biodiversity in a biodiversity hotspot that has been delineated specifically based on the presence of high lichen diversity compared to the rest of the ecoregion. A critical avenue for further study involves determining whether the DRBH is also a hotspot for other groups of obligate symbiotic organisms.

It should be noted that many of the results presented here pertaining to patterns and trends of lichen biodiversity have previously been hypothesized, discussed anecdotally, or validated via studies that did not cover the entire lichen biota. Thus, this study constitutes an important quantitative analysis of lichen diversity and distributions in a biodiversity hotspot, and is, in-so-far as we are aware, unique for any area

outside of Europe. As such, we hope that the methods, both sampling design and analyses, employed herein will serve as a useful model for future work in other areas of North America and abroad. In this manner, establishment of a robust body of scientific literature on lichen biodiversity, via studies the results of which can be directly compared, functions as a critical primary step to affect parity between the biodiversity data available for lichens and those of other macroscopic organisms, such as birds, mammals, and vascular plants.

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APPENDIX I: New lichens, allied, and lichenicolous fungi encountered during the DRBH inventory

***Albemarlea* Lendemer & R.C. Harris gen. nov.**
Mycobank #815,461

Figures 10 and 11

Diagnosis. – A distinct genus of crustose lichenized ascomycetes with biatorine apothecia, *Fuscidea*-type asci that are polysporous and contain many hyaline, ellipsoid, simple ascospores, a coccoid photobiont, conspicuous superficial macropycnidia with narrowly fusiform two-celled hyaline macroconidia, and inconspicuous immersed micropycnidia with curved or bent rod-shaped simple hyaline microconidia.

TYPE: *Albemarlea pamlicoensis*
Lendemer & R.C. Harris

Etymology. – The epithet “*Albemarlea*” commemorates the Albemarle-Pamlico Peninsula of North Carolina, the only area of the Mid-Atlantic Coastal Plain (MACP) where the genus was found during our inventory. It concurrently commemorates the Albemarle Sound, which is a large body of water to the north of the Albemarle-Pamlico Peninsula. Bull Neck Swamp, where the only known population of this genus occurs, is a protected area that includes the largest undeveloped shoreline remaining on the Albemarle Sound.

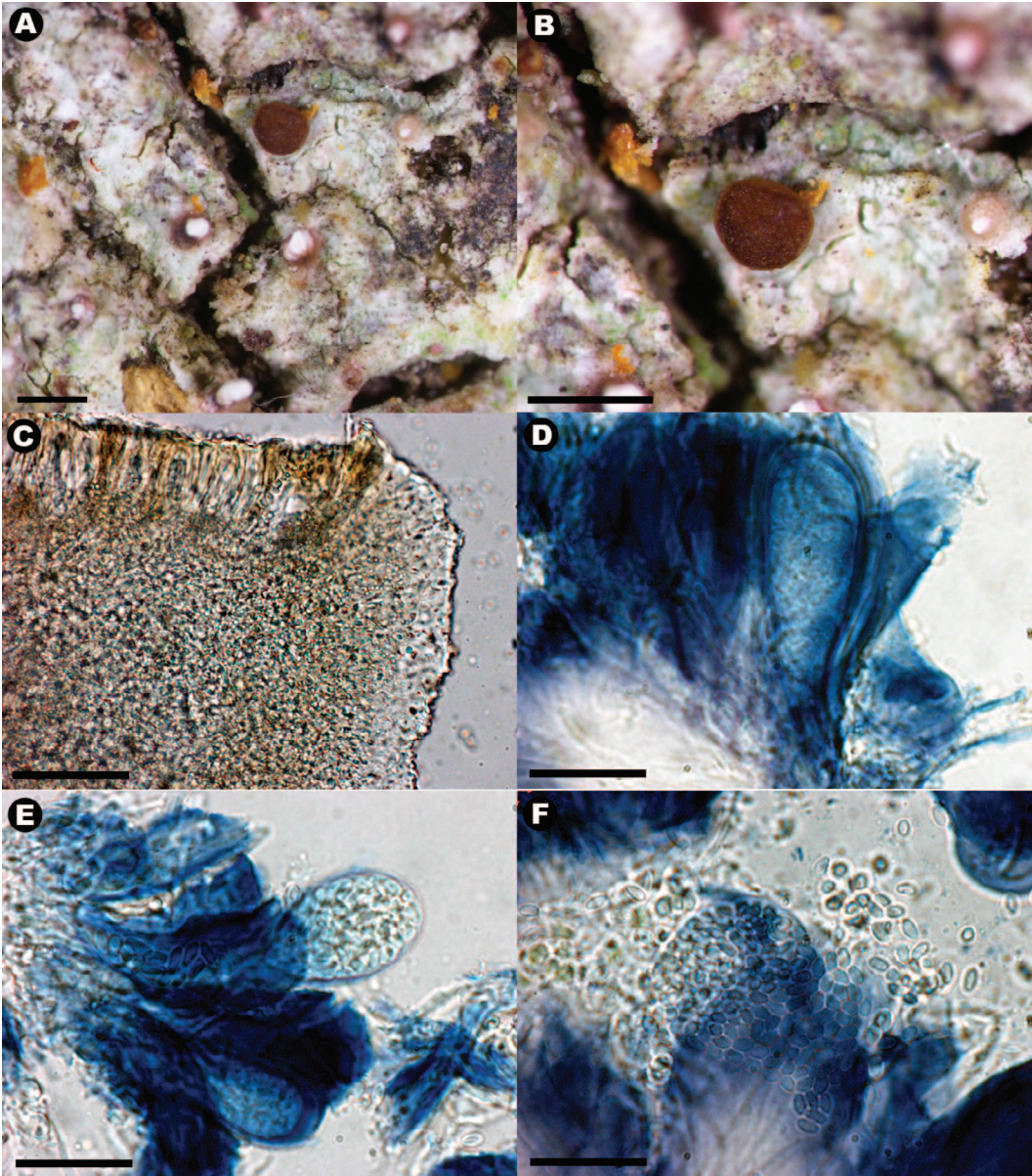


Figure 10. *Albemarleia parmicoensis* (all from the holotype). A. Gross morphology of the thallus illustrating apothecia and conspicuous macropycnidia. B. Detail of apothecium. C. Transverse section of apothecium in water. D. Intact ascus in KI. E. Dehiscing ascus in KI. F. Detail of ascospores in KI. Scale bars = 0.5 μ m in A and B, 50 μ m in C, and 20 μ m in D–F.

Discussion. – The phenomenon of polyspory, or the production of more than eight ascospores per ascus, has been the subject of considerable interest in lichenology (Hafellner 1993, 1995; Reeb et al. 2004). Presumably this is due, in part, to the fact that researchers who study lichens are typically confronted with nearly uniform

monotonous numbers of ascospores, so that when a species producing an unusual number is encountered, it immediately stands out as different. The occurrence of polyspory in lichen-forming fungi was recently summarized by Aptroot and Schumm (2012). Among the families and genera discussed by those authors, *Maronea*

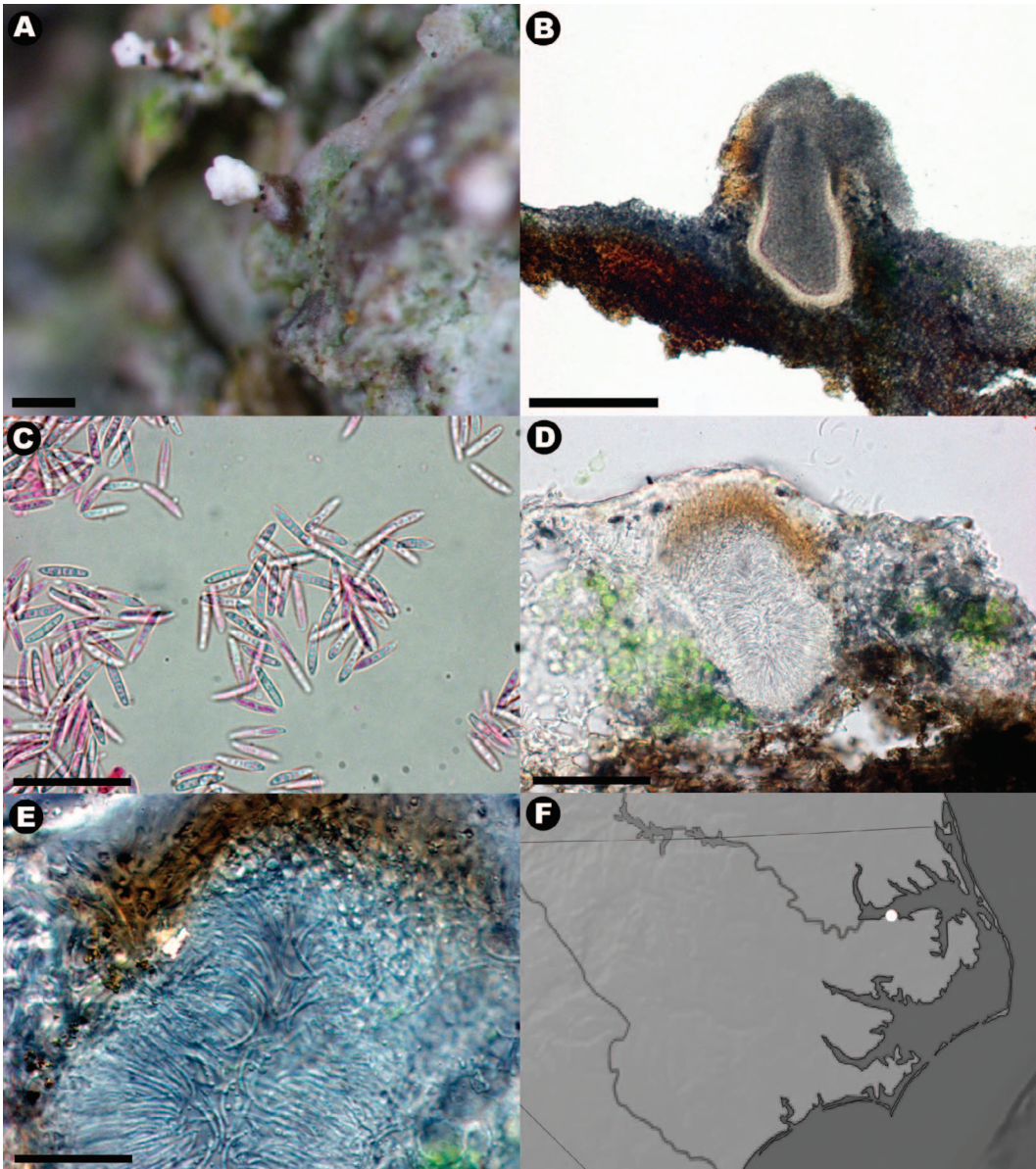


Figure 11. *Albemarlea pamlicoensis* pycnidia (A–E, all from the holotype) and location of the type locality. A. Detail of macropycnidium with mass of conidia attached to the ostiole. B. Transverse section of macropycnidium in water. C. Macroconidia in phloxine. D. Transverse section of micropycnidium in water. E. Detail of micropycnidium also illustrating microconidia in water. F. Geographic distribution of *A. pamlicoensis*. Scale bars = 0.2 mm in A, 200 µm in B, 50 µm in D, and 20 µm in C and E.

is similar to the new genus in having discoid apothecia (vs. perithecia or perithecioid-apothecia), *Fuscidea*-type asci, and numerous hyaline, simple ascospores per ascus (vs. smaller numbers greater than eight, such as 12, 24, 36, etc.). The new genus is readily distinguished from

Maronea by its biatorine apothecia (vs. lecanorine apothecia with thalline margins) and the presence of conspicuous, superficial macropycnidia that produce hyaline, two-celled macroconidia, together with inconspicuous immersed micropycnidia that produce hyaline, curved,

simple microconidia. In some respects, the apothecia and apothecial anatomy of the new genus resemble *Piccolia*, and, although untested with molecular data, we have tentatively considered that genus to be related to the Fuscidaeae based on ascus type (see Hafellner 1995). The apothecia of *Piccolia* contain orange, red, or yellow pigments that are strongly K^+ purple or red, and the conidia (documented in *P. conspersa* (Fée) Hafellner and *P. nannaria*; Hafellner 1995, Lendemer and Harris 2014b) are simple and ellipsoid (vs. fusiform and septate or bent-fusiform and simple). As we are unaware of any other lichen that possesses the aforementioned characters, we here describe it as a new genus with a tentative placement in the Fuscidaeae pending further study with molecular methods.

***Albemarlea pamlicoensis*
Lendemer & R.C. Harris sp. nov.**
Mycobank #815,462

Diagnosis. – A lichen-forming ascomycete with a crustose thallus, coccoid green photobiont, biatorine apothecia, *Fuscidea*-type asci containing many simple, ellipsoid, hyaline ascospores, conspicuous macropycnidia producing hyaline, narrowly fusiform, two-celled macroconidia, and inconspicuous micropycnidia immersed in the thallus and producing hyaline, bent or curved, rod-shaped simple macroconidia.

TYPE: USA, NORTH CAROLINA. Washington Co.: Bull Neck Swamp, south of Hufton Rd., 0.1–0.5 mi west of junction with Old North Bridge Rd., 35°57'50"N 76°26'33"W, 2 ft., upland mixed hardwood forest of *Fagus*, *Quercus*, *Acer*, *Ilex* with *Symplocos*–*Vaccinium* understory, 23 March 2013, on *Fagus* base, J.C. Lendemer et al. 36427 (NY!, holotype).

Description. – *Thallus* crustose, corticolous, greenish-gray, continuous, thin to thick, forming large continuous patches 7–15 cm in diameter, without soredia or isidia; prothallus indistinct, visible as a dark stain near the thallus margins. *Apothecia* biatorine, plane, circular in outline, sessile, reddish-brown in color, 0.3–0.5 mm in diameter, margins thin and slightly paler than the disc, quickly excluded with age; *discs* dark reddish-brown, epruinose; *epihymenium* hyaline to light tan, indistinct; *hymenium* 20–50 μ m, hyaline, not interspersed; *paraphyses* slender, not or little branched, not distinctly expanded at the apices, *hypothecium* 100- to 230- μ m thick,

hyaline, interspersed with oil droplets; *exciple* 50–70- μ m thick, composed of thin radiating hyphae embedded in a thick gelatinous matrix, hyaline or except for a reddish-brown pigment in the outermost layer of cells. *Asci* short, clavate, *Fuscidea*-type, 50–80 $\times$ 20–40 μ m; *ascospores* ellipsoid, simple, hyaline, many per ascus, thin walled, ca. 3.8–4.8 $\times$ 1.9–2.3 μ m. *Pycnidia* of two types: *macropycnidia* abundant, conspicuous, raised above the thallus surface, walls reddish-brown, 250–300 $\times$ 50–70 μ m; *macroconidia* forming a distinct white mass billowing out of the ostiole, narrowly fusiform, hyaline, one septate (rarely becoming two septate), 7.7–9.7 $\times$ 1.6–1.9 μ m; *micropycnidia* sparse(?), inconspicuous, immersed in the thallus, walls hyaline, but becoming brown pigmented near the ostiole, 100–150 $\times$ 50–70 μ m; *microconidia* rod-shaped, weakly to strongly bent and curved, simple, hyaline, 8–9.5 $\times$ 1.0–1.5 μ m. *Photobiont* a coccoid green alga, cells 7–10 μ m in diameter.

Chemistry. – No substances detected. Spot tests: K^- , C^- , KC^- , P^- , UV^- .

Etymology. – The epithet refers to the Pamlico Sound, a body of water located to the south of the type locality on the Albemarle-Pamlico Peninsula. The binomial *A. pamlicoensis* is intended to pay homage to the importance of the Albemarle-Pamlico Peninsula in serving as the primary reservoir for MACP lichen biodiversity.

Ecology and distribution. – Despite having surveyed more than 200 sites in the MACP, and revised thousands of Coastal Plain voucher specimens, the new species is known only from one robust population that was found growing on the base of a single mature American beech (*Fagus grandifolia*) at the type locality (Figure 11F). The type locality is an unusual inland, upland habitat with a relatively mature hardwood forest that is surrounded entirely by swamp forests that host very different vascular plant and lichen communities. We did not find other populations at any of the sites with similar natural communities (Merchants Millpond, North Carolina; Donnelly WMA, South Carolina).

Discussion. – In the field, *A. pamlicoensis* is most likely to be confused with sympatric crustose lichens that produce sporodochia (e.g., *Dictyocatenuata alba*, *Xyleborus nigricans*), because the macropycnidia that are raised well above the surface of the thallus tend to produce masses of macroconidia around the

ostiole, thus giving the superficial appearance of sporodochia. When first located in the field, the new taxon was assumed to be the first fertile material of *D. alba*, a species easily distinguished by its *Trentepohlia* photobiont and sporodochia that are typically elevated on stalks (Lendemer and Harris 2004, Diederich et al. 2008).

Further study of the new taxon revealed the unusual combination of morphological characters, unlike any other polysporous lichen of which we are aware (see, e.g., Hafellner 1993, 1995). The *Fuscidea*-type asci suggest a relationship to *Maronea*; however, members of that genus have lecanorine apothecia and produce secondary compounds. As was suggested by colleagues (J. Hafellner and T. Spribille, pers. comm.), the apothecia of *A. pamlicoensis* are internally somewhat similar to *Sarcosagium campestre* (Fr.) Poetsch and Schied., although that species occurs on soil in northern temperate regions and noticeably differs from *A. pamlicoensis* in having asci with narrow I^+ plugs in the tips (Hafellner 1995; Figure 10).

The internal anatomy of the apothecia, including the ascus type, of *Albemarlea* is also very similar to that of the genus *Piccolia*, particularly *P. conspersa* and *P. nannaria*. The new taxon is not likely to be confused with members of that genus on account of the very different conidia and the absence of orange or red, K^+ red/purple pigments in the apothecia (Hafellner 1995, van der Broeck et al. 2013).

***Arthonia agelastica* R.C. Harris &
Lendemer sp. nov.**
Mycobank #815,463

Figures 12 and 13

Diagnosis. – A species of *Arthonia* Ach. s. lat. on *Lecanora louisianae* B. de Lesd. causing some bleaching or discoloration of the host thallus or less often causing no obvious damage. *Ascomata* light to dark brown, immersed, occurring in scattered to rarely $\pm$ confluent groups. *Ascospores* two (three) septate, macrocephalic, $13\text{--}14.7\text{--}16.7 \times 5.2\text{--}6.0\text{--}7.5 \mu\text{m}$, halonate.

TYPE: USA, NORTH CAROLINA. Tyrrell Co.: Pocosin Lakes National Wildlife Refuge, Frying Pan Boating Access, south of Frying Pan Rd., 6 mi east of junction with NC 94, $35^\circ 48' 12''\text{N}$ $76^\circ 06' 30''\text{W}$, swamp forest of young mixed

hardwoods (*Acer*, *Liquidambar*, *Magnolia virginiana*, *Ilex*) with sparse *Taxodium*, 10 December 2012, on *Lecanora louisianae* on fallen branch, R.C. Harris 58367 (NY!, holotype).

Description. – *Ascomata* immersed in thallus of *Lecanora louisianae*, in groups of few to many ascomata, light brown to dark brown, but sometimes discolored and blackish, epruinose, emarginate, 130- to $185\text{--}\mu\text{m}$ across, $100\text{--}\mu\text{m}$ high; *epihymenium* brown; *hymenium* colorless; *hymenial* gel I^+ orangish, KI^+ blue; *paraphyses* slender, weakly expanded at tips with brown caps; *hypothecium* colorless. *Asci* initially broadly clavate, more elongate at maturity, with tiny KI^+ apical ring, with 8 spores; *ascospores* colorless becoming brown and warted in age, two (three) septate, macrocephalic, $13\text{--}14.7\text{--}16.7 \times 5.2\text{--}6.0\text{--}7.5 \mu\text{m}$, halonate. *Pycnidia* (seen only once), immersed, $\pm$ globose, with pale yellow brown wall, ca. $60\text{--}\mu\text{m}$ across; *conidia* bacillar, hyaline, $3.5\text{--}5 \times 1.2\text{--}1.5 \mu\text{m}$.

Etymology. – The epithet “*agelastica*” (=disposed to herd together) refers to the tendency of the ascomata to occur in discrete groups, or herds, on the thallus of the host.

Chemistry. – No substances detected. Spot tests: K^- , C^- , KC^- , P^- , UV^- .

Ecology and distribution. – *Arthonia agelastica* is evidently an obligate parasite on thalli of *Lecanora louisianae*, a crustose lichen that is common and widespread throughout the Coastal Plain of southeastern North America. The host typically occurs on the bark and branches of hardwood trees or shrubs, particularly in open swamp or coastal habitats.

It is notable that, although *Lecanora louisianae* is nearly ubiquitous from Delaware to Texas (and as far south as Hendry County in Florida), *A. agelastica* appears to have a considerably more restricted distribution (Figure 13). A survey of the 261 collections of *L. louisianae* held at NY located only five records in addition to those collected during our fieldwork on the Dare Peninsula. Of the 126 collections from Florida, only two were found to host *A. agelastica*. Similarly, only 3 collections of *A. agelastica* were found among the 64 collections of *L. louisianae* from North Carolina. Our search of the 71 additional collections of *L. louisianae* from other states in eastern North America failed to reveal any additional material of *A. agelastica*.

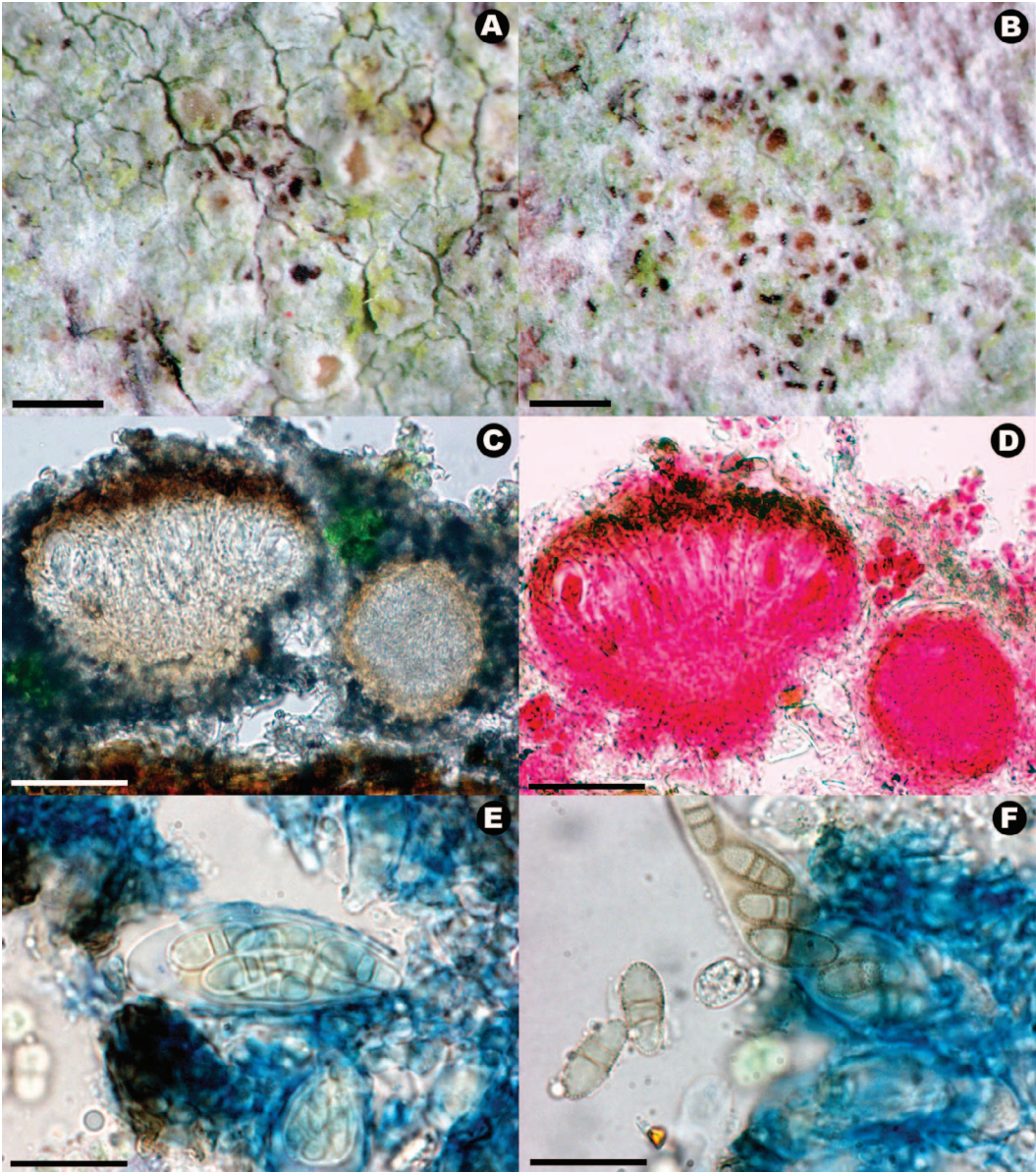


Figure 12. *Arthonia agelastica* (all from Harris 58367). A. Small group of ascomata associated with poorly developed apothecia of the host. B. Well-developed group of ascomata. C and D. Transverse section in water (C) and fuchsin (D) of apothecium (left) and pycnidium (right) on host thallus. E. Ascus with intact ascospores in iodine. F. Mature or postmature ascospores that have turned brown and are mounted in iodine. Scale bars = 0.5 mm in A, 0.25 mm in B, 100 µm in C and D, and 20 µm in E and F.

Discussion. – *Arthonia agelastica* is readily identifiable by its two-septate macrocephalic ascospores and ascomata that are immersed in the thallus of *Lecanora louisianae*. A number of other species of *Arthonia* have been reported to

occur on various *Lecanora* species (Lawrey and Diederich 2011). Of these species, only *A. subfuscicola* (Linds.) Triebel has been reported from members of the *L. subfusca* group (in a broad sense), specifically from *L. carpineae* (L.)

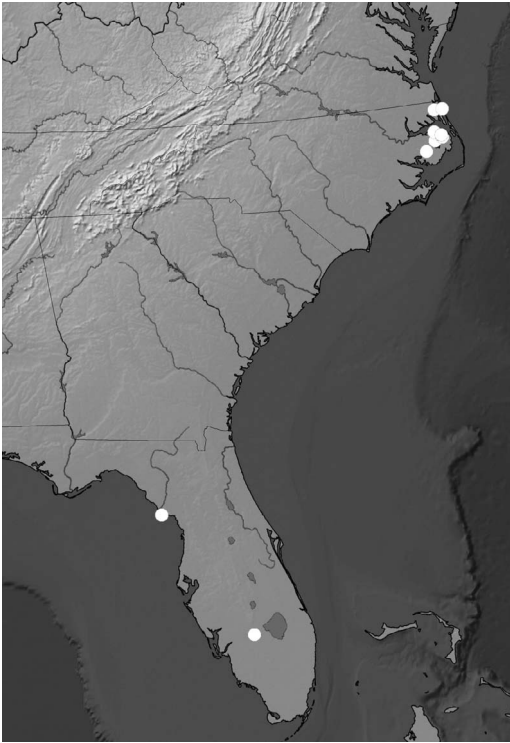


Figure 13. Geographic distribution of *Arthonia agelastica*.

Vainio and *L. pallida* (Schreb.) Rabenh. (Triebl et al. 1991). *A. subfuscicola* differs from the new species in occurring mainly in the hypothecium of the apothecia of the host (vs. on the thallus), in having a dark hypothecium (vs. a hyaline one), and in having three-septate (vs. two-septate) ascospores (Triebl et al. 1991).

Additional specimens examined (all on thalli of *Lecanora louisianae*). – **FLORIDA.** Glades Co.: Ortona Cemetery, along SR 78, 1 mi west of CR 78A, 30 March 1998, on branch of *Quercus*, *R.C. Harris 42119-A* (NY). Levy Co.: Suwannee National Wildlife Refuge, Shell Mound County Park at west end of Co. Rd. 326, 3 December 1993, on branch, *R.C. Harris 31477* (NY). **NORTH CAROLINA.** Carteret Co.: Cedar Island National Wildlife Refuge, south of Lola Rd. ~1.3 mi southeast of junction with NC 12, 24 October 2012, on *Ilex*, *J.C. Lendemer et al. 38416* (NY). Currituck Co.: Currituck Banks National Estuarine Research Reserve, west side adjacent to Currituck Sound, 0–1 mi north of terminus of NC 12 in Corolla, 14 April 2012, on *Quercus*, *R.C.*

Harris 57272-A (NY); North River Game Land, west of Maple Rd., 0.5 mi north of intersection with US 158, 12 April 2012, on *Acer*, *J.C. Lendemer 30715-A* (NY). Dare Co.: Alligator River National Wildlife Refuge, west of Brier Hall Rd., 1.6 mi north of junction with US 64, 8 December 2012, on fallen branch, *R.C. Harris 58113-A* (NY); Alligator River National Wildlife Refuge, west of Buffalo City Rd., 1.2 mi south of US 64, 12 December 2012, on *Acer*, *R.C. Harris 58623* (NY); Alligator River National Wildlife Refuge, southeast of junction of Spring Rd. and Navy Shell Rd., 19 March 2014, on *Acer*, *J.C. Lendemer et al. 42658* (NY); Buxton Woods Coastal Reserve, southwest of terminus of Old Doctor Rd., west of Lookout Loop Trail, 18 August 2013, on *Vitis*, *J.C. Lendemer 35850-A* (NY); Cape Hatteras National Seashore, just west of Ramp 30, west of NC 12, north of Avalon, 19 March 2013, on *Myrica*, *J.C. Lendemer 36309A* (NY); Kill Devil Hills, Nags Head Woods Ecological Preserve, along Old Nags Head Woods Rd., 29 September 1993, on branches, *W.R. Buck 24121-A* (NY). Hyde Co.: Pocosin Lakes National Wildlife Refuge, south of New Lake Rd./SR1303, 7 mi northeast of junction with Higginsport Rd./SR 1302, 11 December 2012, on *Acer*, *J.C. Lendemer 34871* (NY); Cape Hatteras National Seashore, north of NC 12, 0.25 mi west of Old Hammock Creek, 20 March 2014, on *Ilex*, *J.C. Lendemer 42746* & *E. Tripp* (NY). Tyrrell Co.: Pocosin Lakes National Wildlife Refuge, Frying Pan Boating Access, south of Frying Pan Rd., 6 mi east of junction with NC 94, 10 December 2012, on twigs, *W.R. Buck 60025* (NY), on upper branch of fallen *Acer*, *R.C. Harris 58371-A* (NY), on fallen branch, *R.C. Harris 58393-A* (NY). Washington Co.: Bull Neck Swamp, Deep Creek Rd., north of junction with Bear Lane, 23 March 2013, on *Acer*, *E. Tripp et al. 4142* (NY); Bull Neck Swamp, south of Hufton Rd. 0.1–0.5 mi west of junction with Old North Bridge Rd., 23 Mar 2013, on *Acer*, *J.C. Lendemer et al. 36471* (NY).

***Arthonia hodgesii* Lendemer & R.C. Harris
sp. nov.**

Mycobank #815,464

Figures 14 and 15

Diagnosis. – Differing from *Arthonia graphidicola* in having a brownish-orange epiphyne-

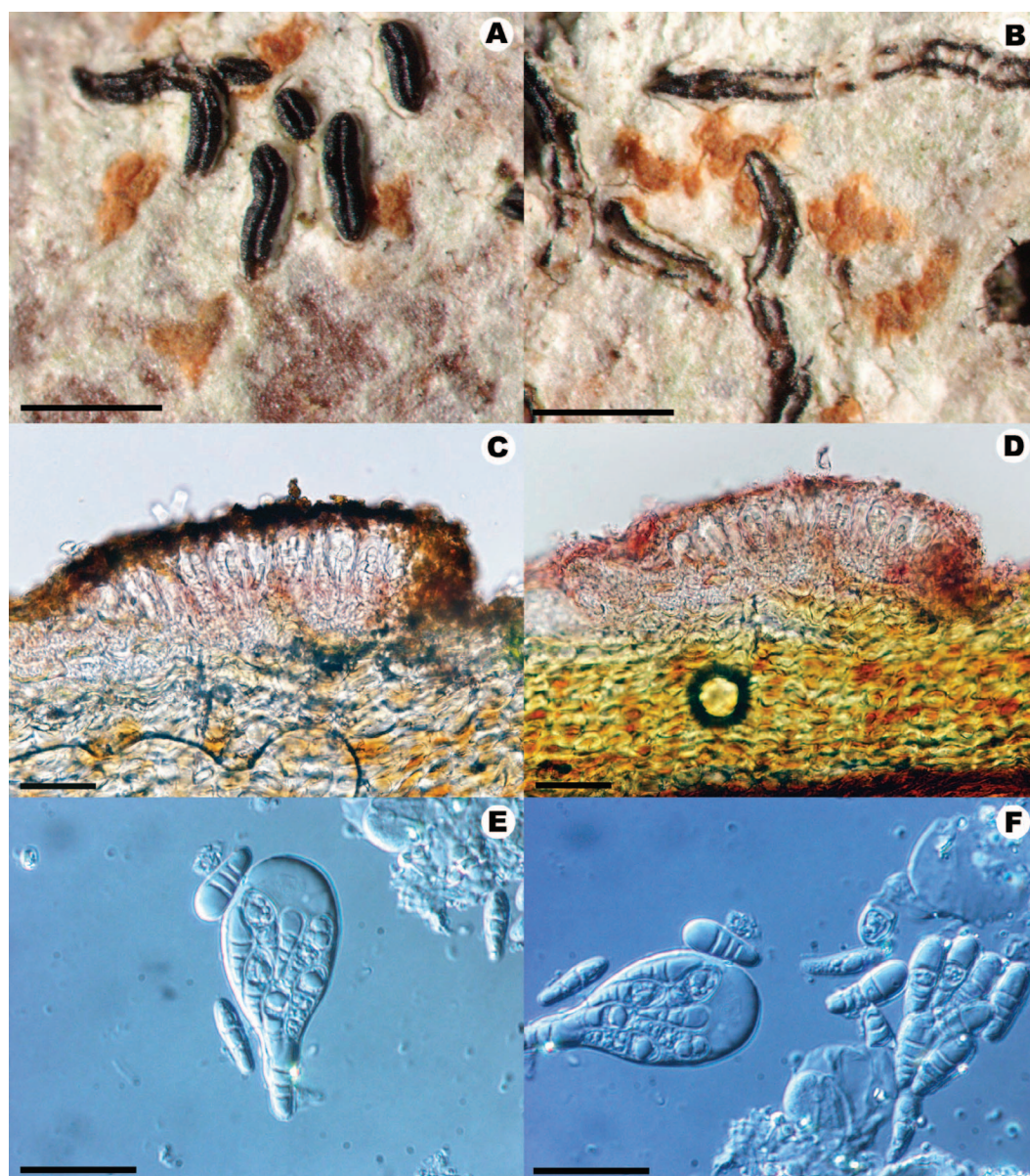


Figure 14. *Arthonia hodesii* (all from the holotype). A and B. Detail of fruiting bodies and infection occurring on thallus of *Graphis lineola*. C. Transverse section of ascoma in water. D. Transverse section of ascoma in K illustrating reaction of pigments. E and F. Ascus and ascospores in water. Scale bars = 500 μ m in A and B, 50 μ m in C and D, and 20 μ m in E and F.

nium that is K^+ magenta (vs. K^+ dull olive) and an I^+ blue (vs. I^-) hymenium.

TYPE: USA, GEORGIA. Dougherty Co.: Chickasawhatchee Wildlife Management Area, 31°29'25"N 84°25'07"W, pond cypress swamp forest, 10 November 2012, on *Graphis lineola* on

branch of *Morella cyrifera*, M.F. Hodges 9228 (NY!, holotype).

Description. – *Ascomata* immersed in thallus of *Graphis lineola*, not producing any visible infection, light brownish-orange, slightly raised above the thallus surface, elongate and irregu-

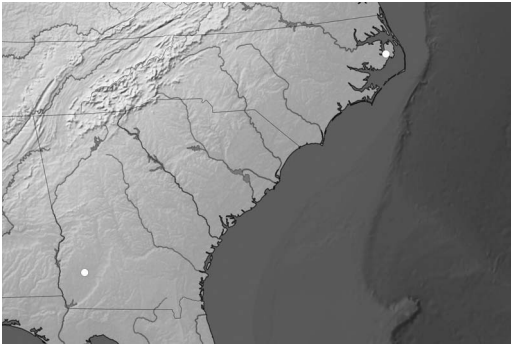


Figure 15. Geographic distribution of *Arthonia hodesii*.

larly shaped $0.25\text{--}0.5 \times 0.1\text{--}0.3$ mm, often somewhat aggregated in a portion of the host thallus; *epihymenium* dark orange-brown pigmented, with the pigment turning K^+ magenta but not dissolving; *hymenium* hyaline, I^+ blue, KI^+ greenish blue; *hypothecium* hyaline; *paraphyses* slender, weakly expanded at tips. *Asci* obovoid to obpyriform, without apical ring, $30\text{--}40 \times 18\text{--}25$ μm ; *ascospores* three septate, hyaline, $\pm$ macrocephalic, becoming brownish and weakly roughened with age, I^- , $(12.4\text{--})12.8\text{--}13.6\text{--}14.3(-15) \times (4.2\text{--})4.5\text{--}5.1\text{--}5.8(-6.8)$ μm ($n = 25$). *Pycnidia* not seen.

Etymology. – The new species is named in honor of Malcolm Hodges, who, together with Sean Beeching, has contributed greatly to our knowledge of the lichen biota of Georgia. Both have an eye for unusual, small, or interesting species and are an asset to the field.

Chemistry. – Anthraquinone pigment in apothecia. Spot tests (pigmented portions): K^+ magenta, KC^- , C^- , P^- , UV^- .

Ecology and distribution. – The new species is known only from two sites in the Coastal Plain of southeastern North America (Figure 15), where it was found growing in swamp forests on thalli of *Graphis lineola* on the bark of small hardwood trees and shrubs. Although the species is inconspicuous, it is readily visible and would likely have been detected if it were more widespread in the region where it occurs.

Discussion. – *Arthonia hodesii* is most similar to *A. graphidicola* Coppins, a species described from *Graphis scripta* (L.) Ach. in Great Britain (Coppins 1989) and subsequently reported from France (Coste 1993) and Spain (Etayo and Diederich 1998). Although both

species have similarly sized three-septate ascospores that are hyaline and macrocephalic, *A. hodesii* differs from *A. graphidicola* in having an orange pigment in epihymenium that is K^+ magenta (vs. a reddish-brown pigment that is K^+ dull olive) and an I^+ blue hymenium (vs. I^-) (*vide* Coppins 1989). The species also differ in their hosts, with *A. graphidicola* occurring on the primarily temperate species, *G. scripta*, and *A. hodesii* occurring on *G. lineola*.

Arthonia diorygmae S. Joshi and Upreti is another lichenicolous species that was recently described from a host belonging to the family Graphidaceae in its traditional sense (Joshi et al. 2013). That species differs from *A. hodesii* in numerous respects, including having circular ascomata and one-septate ascospores. The authors described *A. diorygmae* as having a brown to olive epihymenium that was “ K^+ slightly purplish” and, thus, it is unclear what type of pigment is present in the species. It should be noted that, in discussing their new species, as well as comparing it in a key to other lichenicolous species, Joshi et al. (2013) did not note the absence of K^+ purple pigments in the epihymenium, as originally reported by Coppins (1989). Thus, those relying on the key published by Joshi et al. (2013) would likely incorrectly key *A. hodesii* to *A. graphidicola*.

Recently, the circumscription of the Graphidaceae has been greatly expanded to include not only the entire Thelotremaataceae, but also several other morphologically divergent families (Rivas Plata et al. 2012). Although we have elected to follow a more conservative taxonomy (Hodkinson 2012), it should be noted that *Arthonia thelotrematis* Coppins has been described from *Thelotrema lepadinum* (Ach.) Ach., a host that would now be placed in the same family as the hosts of *A. graphidicola* and *A. hodesii*. As described by Coppins (1989), *A. thelotrematis* differs from *A. hodesii* in having reddish-brown epihymenium that is K^+ greenish, a similarly pigmented hypothecium (vs. hyaline in *A. hodesii* and *A. graphidicola*), as well as slightly smaller ascospores ($11\text{--}14 \times 4.5\text{--}5.5$ μm). Based on the available literature, *A. hodesii* appears to be only the third species of *Arthonia* described from members of Graphidaceae in the traditional sense of that family.

Additional specimen examined. – **USA, NORTH CAROLINA. Dare Co.:** Alligator River

National Wildlife Refuge, west of Whipping Creek Rd., 0.5 mi north of junction with Chip Rd., 23 March 2014, on *Graphis lineola* on dead sapling, *R.C. Harris 60261-B* (NY).

***Arthonia stevensoniana* R.C. Harris & Lendemer sp. nov.**
Mycobank #815,465

Figure 16

Diagnosis. – *Arthonia* in hymenium of *Haematomma accolens* (Stirt.) Hillmann with brown hypothecium, dark green to green-black in KOH, hymenium I^+ orange and ascospores $10\text{--}14 \times 4\text{--}5 \mu\text{m}$.

TYPE: USA, GEORGIA. Candler Co: Charles Harold TNC Preserve, 0–0.25 mi north of Salem Church Rd., west side of Stocking Head Creek, $32^\circ 25' 01''\text{N}$, $82^\circ 04' 09''\text{W}$, bottomland mixed hardwood forest (*Nyssa*, *Acer*, *Quercus*) with pine (*Pinus*), 22 December 2009, in hymenium of apothecia of *Haematomma accolens* on *Acer*, *J.C. Lendemer et al. 21768* (NY!, holotype).

Description. – *Ascomata* in hymenium of apothecia of *Haematomma accolens*, black, flush with surface of host hymenium or slightly raised, 0.08– (immature) to 0.3-mm across, one to many per apothecium, sometimes coalescing so that entire disk of host is blackened; *epihymenium* brown; *hymenium* brown streaked, lower part dark greenish in KOH, I^+ orange, KI^+ greenish blue; *hypothecium* brown, dark greenish or greenish black in KOH; *paraphyses* mostly indistinct, thin, some weakly swollen at tip with a dark cap. *Asci* obovoid to obpyriform, without apical ring, $25\text{--}40 \times 12\text{--}17 \mu\text{m}$; *ascospores* one septate, hyaline, $\pm$ soleiform, becoming brownish and weakly roughened with age, upper cell slightly broader and longer than lower, with an I^+ orangish sheath, $(9.4\text{--})10.1\text{--}11.1\text{--}12.1\text{--}(13.7) \times (3.7\text{--})3.9\text{--}4.3\text{--}4.8\text{--}(5.6) \mu\text{m}$ ($n = 52$). *Pycnidia* black, immersed in host hymenium, ca. $35\text{--}45 \mu\text{m}$ across, upper part of wall brown, lower part paler; *conidia* hyaline, narrowly fusiform, ca. $3.7\text{--}4.5\text{--}(5.2) \times 1.1\text{--}1.6\text{--}(1.8) \mu\text{m}$.

Etymology. – The epithet of the new species honors Robert Louis Stevenson (1850–1894), author of *Treasure Island* and *Strange Case of Dr. Jekyll and Mr. Hyde*. The reasoning for this eponymy is twofold; first the *Arthonia* is a pirate that takes over the apothecia of the host thallus, and second that the black spots on the red discs

of *Haematomma* are reminiscent of the practice in *Treasure Island* of pirates giving the black spot as a threat of harm or death. It is also worth noting that Stevenson was a lover of islands, and traveled with his father throughout Scotland to examine the many lighthouses that his family had designed. Islands and lighthouses are iconic features of the region where the species grows, which was once home to many notorious pirates.

Ecology and distribution. – *Arthonia stevensoniana* appears to be endemic to the southeastern Coastal Plain of eastern North America, where it is known from a small number of inland swamp forest sites scattered across Georgia and North Carolina (Figure 16F). Interestingly, it is restricted to the apothecia of *Haematomma accolens*, a species that is common and widespread in portions of the Coastal Plain (Brodo et al. 2008). We suspect that the species is host specific and rare, given the frequency of *Haematomma* species in the region where it occurs, and the large amount of study that the genus has received (see below).

Discussion. – Species of the crustose lichen genus *Haematomma*, and the lichenicolous fungi that occur on them, have been the subject of considerable study and taxonomic treatments (see, e.g., Culberson 1963, Asahina 1964, Rogers 1982, Rogers and Bartlett 1986, Culberson et al. 1986, Kalb et al. 1995, Elix 2004, Nelsen et al. 2006, Brodo 2007, Brodo et al. 2008, Lumbsch et al. 2008). Similarly well studied are the lichenicolous species of *Arthonia*, which often form conspicuous infections on their host lichens and, thus, are routinely collected even by those not specializing in lichenicolous fungi (see, e.g., Santesson 1993, Grube et al. 1995, Hafellner 1995, Grube and Matzer 1997, Wedin and Hafellner 1998, Santesson et al. 2004). Given the robust body of literature devoted to these groups, and the large number of specimens of *Haematomma* that exist in herbaria, it was surprising to discover a previously unknown *Arthonia* that forms conspicuous black infections on the apothecia of *Haematomma*.

Among the lichenicolous fungi that occur on *Haematomma*, only *Arthonia haematommatum* Kalb and Hafellner from New Zealand also occurs in the hymenium of the host. However, that species differs from *A. stevensoniana* in having three-septate (vs. one-septate) ascospores, and in occurring on a different host with a different geographic distribution (*H. accolens* vs. *H. alpi-*

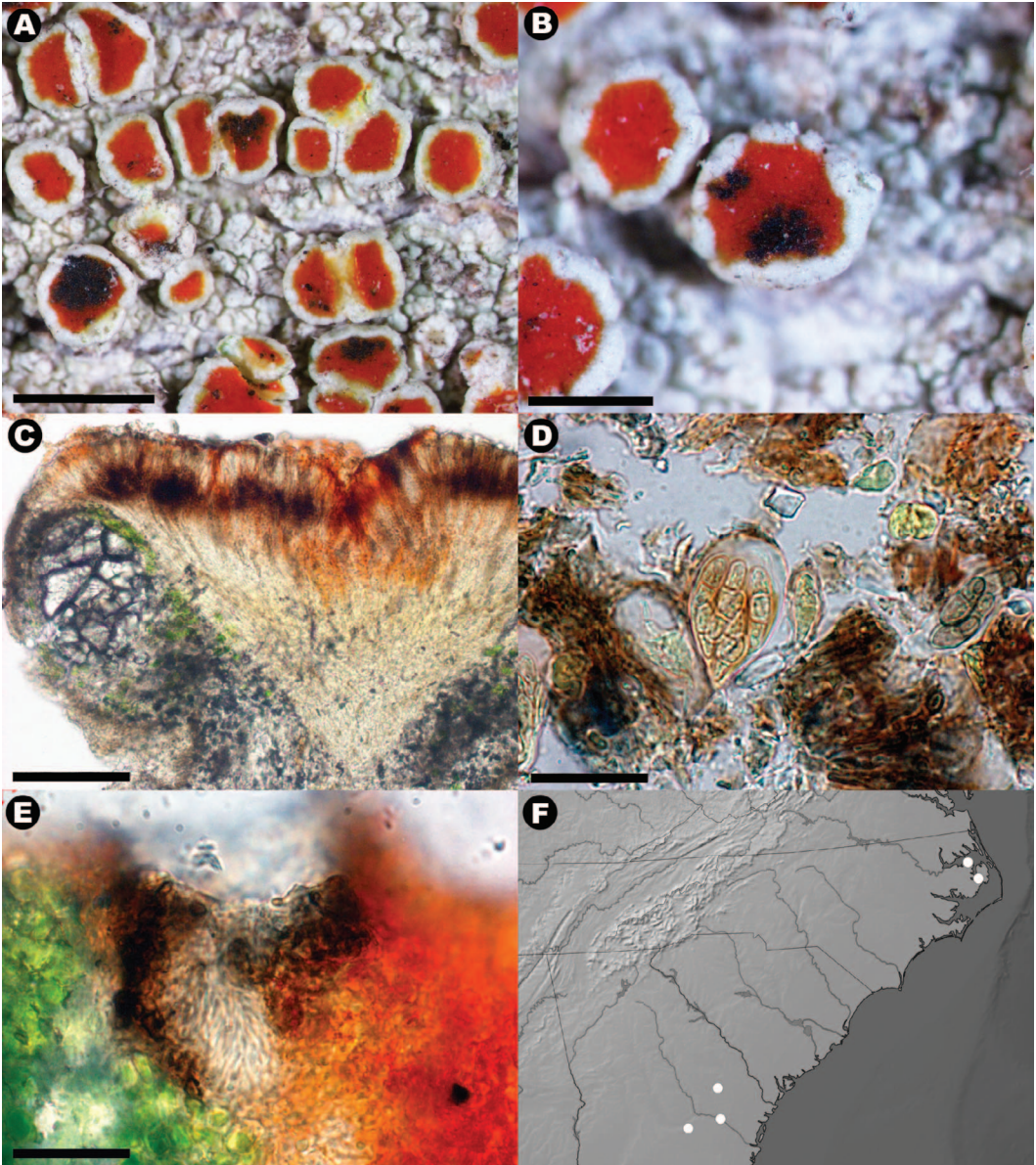


Figure 16. *Arthonia stevensoniana* morphology (A–E, all from the holotype), and geographic distribution. A. Gross morphology of infection in apothecia of *Haematomma accolens*. B. Detail of infection on apothecium of *H. accolens*. C. Transverse section of host apothecium with immersed ascoma, mounted in water. D. Ascus and ascospores in water. E. Transverse section of pycnidium in water. F. Geographic distribution of *A. stevensoniana*. Scale bars = 0.5 mm in A and B, 200 μ m in C, and 20 μ m in D and E.

num R.W. Rogers and *H. babingtonii* A. Massal.; see Kalb et al. 1995). Although other lichenicolous fungi may blacken the apothecial discs of *Haematomma* species, none of these produce ascomata and have one-septate ascospores.

There are several species of *Arthonia* with one-septate ascospores that blacken the apothecia of other related lichen genera, such as *Lecanora* and *Rhizoplaca*. In addition to occurring on other hosts, two such species (*A.*

apotheciorum (A. Massal.) Almq. occurring on members of the *Lecanora dispersa* group and *A. Clemens* (Tul.) Th. Fr. occurring on *Rhizoplaca*) differ from *A. stevensoniana* in having hyaline rather than brown hypothecia. The remaining species (*A. galactinaria* Leight. [= *A. apotheciorum*?] occurring on *L. dispersa* (Pers.) Sommerf., *A. lecanorina* (Almq.) R. Sant. Occurring on *L. albella* (Pers.) Ach.) have dark hypothecia and ascospores similar in size to those of *A. stevensoniana*, and thus must be separated based on their host preference. Although further study of this group is needed, it should be noted that neither *L. albella* nor *L. dispersa* are sympatric with *Haematomma accolens* in North America, or evidently with *A. stevensoniana*.

Additional specimens examined (all in the hymenium of apothecia of *Haematomma accolens*). – **USA, GEORGIA. Coffee Co.:** Broxton Rocks Ecological Preserve, 9 mi northeast of Broxton, falls of Rocky Creek, 8 February 2003, on *Quercus*, *R.C. Harris* 47039 (NY). **Pierce Co.:** Little Satilla Wildlife Management Area, Knight Rd., ca. 1 mi east of Offerman between Zero Bay and Sixty Foot Branch of Little Satilla River, 21 December 2009, on *Acer*, *J.C. Lendemer et al.* 21533 (NY). **USA, NORTH CAROLINA. Dare Co.:** Alligator River National Wildlife Refuge, west of Whipping Creek Rd., 0.5 mi north of junction with Chip Rd., 23 March 2014, on dead sapling, *R.C. Harris* 60260 (NY). **Tyrrell Co.:** Palmetto-Peartree Preserve, northwest of junction of Loop Rd. and Canoe Pier Spur, 0.5 mi north of junction of Loop Rd. and Pot Licker Rd., 12 December 2012, on *Acer*, *R.C. Harris* 58567 (NY).

***Lichenochora haematommatus* R.C. Harris & Lendemer sp. nov.**
Mycobank #815,466

Figure 17

Diagnosis. – *Lichenochora* forming galls on the thallus and apothecia of *Haematomma persoonii* that contain few to many perithecia in various stages of maturity. Ascospores initially colorless, finally brown, broadly ellipsoid, one septate, constricted at the septum, (12–) 12.9–14.0–15.0(–16.4) $\times$ (7.1–) 7.5–8.0–8.5(–9.3) μm , with a punctate perispore.

TYPE: **USA, NORTH CAROLINA. Dare Co.:** Cape Hatteras National Seashore, east of Lighthouse Visitor Center, 35°15'04"N, 75°31'29"W,

elevation 7 ft., maritime forest of *Pinus-Juniperus-Quercus* with *Ilex vomitoria* understory, 18 March 2013, on *H. persoonii* on *Quercus*, *J. C. Lendemer* 36123 (NY!, holotype).

Description. – *Lichenicolous fungus* forming galls on thallus and apothecia of *H. persoonii*; galls concolorous with the host thallus, $\pm$ orbicular or irregular in shape, containing one to many perithecia, 0.2-mm across (single perithecium per gall) to 1.0-mm across (multiple perithecia per gall). *Perithecia* immersed to varying levels in galls, with only black tips visible, typically solitary but occasionally two to three perithecia becoming fused, black, pyriform, 125- to 130- μm wide, 150- to 200- μm tall, with black wall of elongated cells, 14- to 23- μm thick; *periphyses* present; *hymenium* filled with numerous oil droplets; *paraphyses* deliquescent. *Asci* $\pm$ cylindrical, uniformly thin walled; *ascospores* hayline, finally brown, occasionally weakly brown when still inside the ascus, broadly ellipsoid, one septate, $\pm$ constricted at the septum initially and becoming markedly so with age, (12–) 12.9–14.0–15.0(–16.4) $\times$ (7.1–) 7.5–8.0–8.5(–9.3) μm ($n = 34$), with a punctate perispore. *Pycnidia* not seen.

Etymology. – The epithet refers to the host genus *Haematomma*, as this appears to be the first member of *Lichenochora* discovered on that host.

Ecology and distribution. – *Lichenochora haematommatus* is so far known only from two sites within a small area of Hatteras Island on the Outer Banks of North Carolina (Figure 17F). It is not uncommon at these sites, and is particularly abundant at the type locality where nearly every thallus of the host species appears to be infected. The restricted distribution of the new species does not appear to be an artifact of collection bias, as its host, *H. persoonii*, occurs throughout much of coastal southeastern North America and often dominates corticolous lichen communities on hardwood shrubs and branches in open, scrubby maritime forests. Despite having inventoried hundreds of sites in the southeastern Coastal Plain, and having made more than 100 collections of *H. persoonii*, the new species remains known only from Hatteras Island. Thus, it is possible that the species may be narrowly endemic to the area, or to the Carolinian Barrier Island ecoregion (see Griffith et al. 2002).

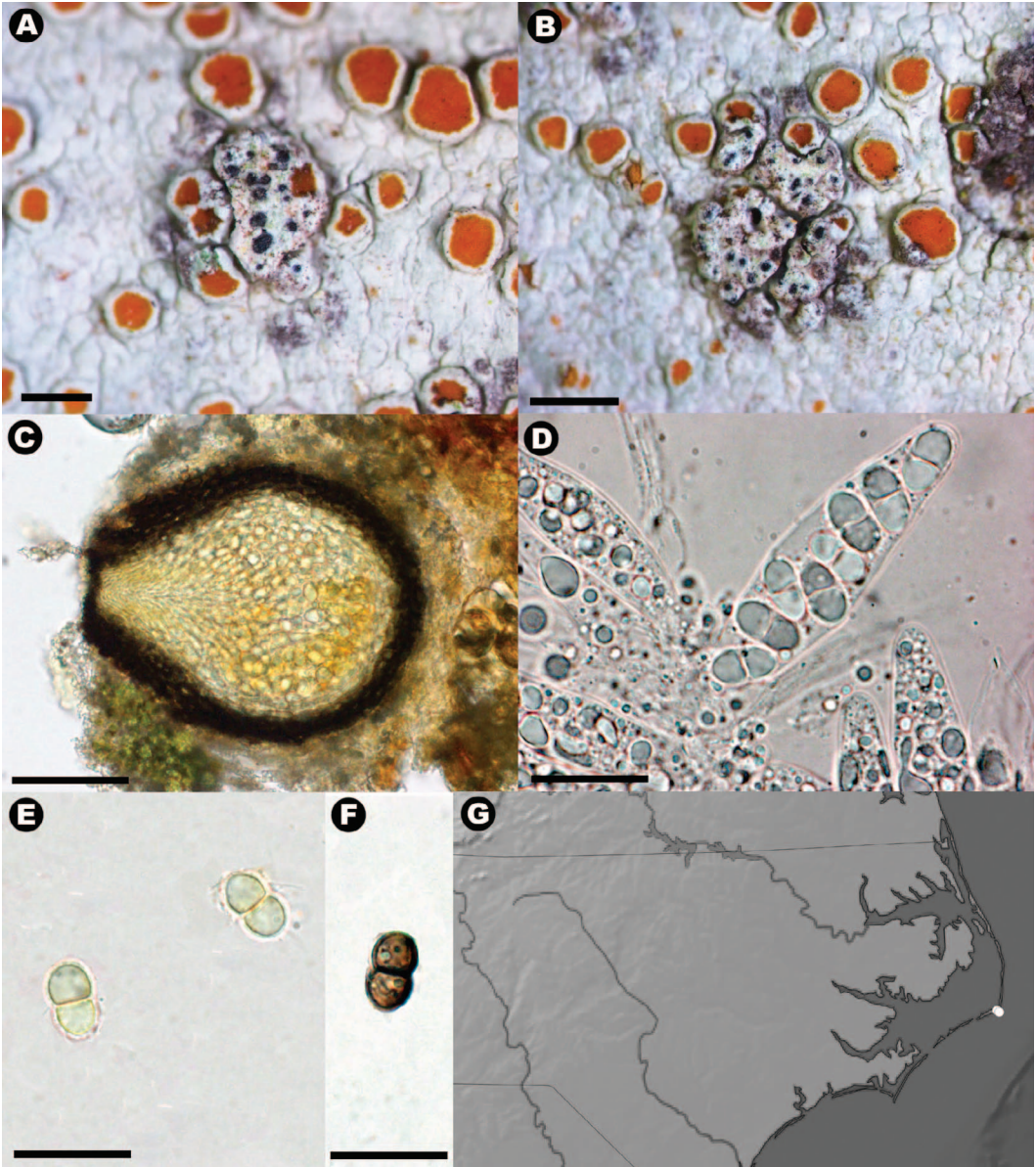


Figure 17. *Lichenochora haematommatus* morphology (A–E) and geographic distribution. A and B. Infection forming conspicuous galls on *Haematomma persoonii* (from Lendemer 36123). C. Transverse section of perithecium in IKI (from Buck 63107). D. Asci and ascospores in water (from Lendemer 36123). E. Hyaline ascospores (from Buck 63107). F. Brown ascospores (from Lendemer 36101). G. Geographic distribution of *L. haematommatus*. Scale bars = 0.5 mm in A and B, 200 μ m in C, and 20 μ m in D–F.

Discussion. – The genus *Lichenochora* (Phylachoraceae) is easily recognized by its perithecia, hymenium that is obscured by oil droplets, deliquescent paraphyses, and uniformly thin-walled asci. Etayo and Navarro-Rosinés (2008)

provided a key to the species of *Lichenochora* known at that time. In that key *L. haematommatus* comes closest to *L. aipoliae* Etayo, Navarro-Ros., and Coppins, a species described from Great Britain that has similar-sized, broad,

ornamented, one-septate ascospores where the cells are of equal size, and which turn brown with age. The new species differs from *L. aipoliae* in having broader ascospores (7–9 μm vs. 5–7 μm) and in host preference (the crustose genus *Haematomma* vs. the foliose genus *Physcia*). Of the species described after 2008, *L. physciicola* (Ihlen and R. Sant.) Hafellner described from Sweden is most similar. Although the ascospores in that species are sized 11–13(–14) $\times$ 7–9 μm (fide Ihlen and Wedin 2005), they nonetheless differ from those of *L. haematommatus* in remaining hyaline (vs. turning brown) and in having a smooth perispore that is not ornamented (vs. a distinctly punctate ornamented perispore). *Lichenochora physciicola* further differs from *L. haematommatus* in its host, occurring on the foliose species *Physcia dubia* (Hoffm.) Lettau rather than crustose *Haematomma*.

Additional specimens examined (all on *H. personii*). – **USA, NORTH CAROLINA. Dare Co.:** same locality as for the type, 18 March 2013, on *Quercus*, J.C. Lendemer 36092-A (NY), J.C. Lendemer 36101 (NY); Cape Hatteras National Seashore, trail from World War II Memorial, 0.5 mi west of Lighthouse Rd., 24 March 2014, on *Quercus*, W.R. Buck 63107 (NY), J.C. Lendemer 43159 (NY).

***Megalaria alligatorensis* Lendemer sp. nov.**
Mycobank #815,467

Figure 18

Diagnosis. – Similar to *Megalaria albocincta* and *M. anaglyptica*, but differing in its smaller and narrower ascospores.

TYPE: USA, NORTH CAROLINA. Hyde Co.: Alligator River National Wildlife Refuge, Chip Rd. 2 mi southwest of junction with Whipping Creek Rd., 35°38'40"N 75°58'42"W, 2 ft., pocosin dominated by *Pinus* and *Gordonia*, with sparse *Acer* and *Magnolia virginiana*, understory of *Cyrilla*, *Ilex glabra*, and *Persea*, 23 March 2014, on *Cyrilla*, J.C. Lendemer et al. 43124 (NY!, holotype).

Description. – *Thallus* crustose, corticolous, greenish-blue, forming small, circular patches 2–3 cm in diameter, areolate, without soredia or isidia; *prothallus* white, fibrous, poorly developed, and visible between the areoles, becoming immersed and darkened at the margin near the growing edge of the thallus; *areoles* small,

$\pm$ dispersed to crowded and becoming confluent, initially globose and convex, but eventually becoming flattened. *Apothecia* biatorine, plane and flat, circular in outline and rarely becoming $\pm$ deformed, sessile, 0.4–1.0 mm in diameter; margins pale, waxy white, contrasting strongly with the coloration of the discs, becoming excluded with age; *discs* dark blue–black, epruinose; *epihymenium* 10- to 20- μm thick, blue-gray pigmented, K[–]; *hymenium* 50- to 80- μm thick, hyaline, not interspersed; *hypothecium* 25- to 50- μm thick, upper portions pigmented purple, K⁺ distinctly blue, lower portions pigmented brownish, K⁺ more intense brown; *exciple* bilayered, comprised of an inner layer 60- to 100- μm thick, comprised of *textura intricata*, lightly brownish pigmented and K⁺ yellow, and an outer layer 40- to 60- μm thick, comprised of thick, gelatinized hyphae densely interspersed with POL⁺ crystals, without pigment and K[–]. *Asci* *Bacidia*-type, cylindrical to clavate, eight-spored; *ascospores* narrowly ellipsoid, often weakly bent to one side, hyaline, one septate, thick walled, not halonate, 12–14 $\times$ 3.8–5.5 μm . *Pycnidia* not seen.

Chemistry. – Atranorin, zeorin, and fumarprotocetraric acid. Spot tests: K⁺ weak yellow, KC[–], C[–], P⁺ orange-red, UV[–].

Etymology. – The epithet refers both to the type locality in the Alligator River National Wildlife Refuge and, more generally, to the Alligator River region of North Carolina where the species occurs.

Ecology and distribution. – The new species is known only from the type locality (Figure 18F), where it was found growing on the bark of a hardwood tree (sweet bay [*Magnolia virginiana* L.]) and an ericaceous shrub (titi [*Cyrilla racemiflora* L.]) in dense shade in the understory of a pocosin. Due to the difficulty in accessing and traversing pocosin peatlands, it is possible that the species is more widespread in the region and has simply been overlooked previously.

Discussion. – Based on the production of zeorin and the presence of a distinctly bilayered exciple, *Megalaria alligatorensis* is most likely related to other tropical species that would have been classified in the genus *Catillochroma* Kalb by Kalb (2007). The circumscription of *Megalaria* Hafellner followed here is the pragmatic one adopted by Fryday and Lendemer (2010), wherein members of *Catillochroma* and *Lopezaria* Kalb and Hafellner were lumped within a

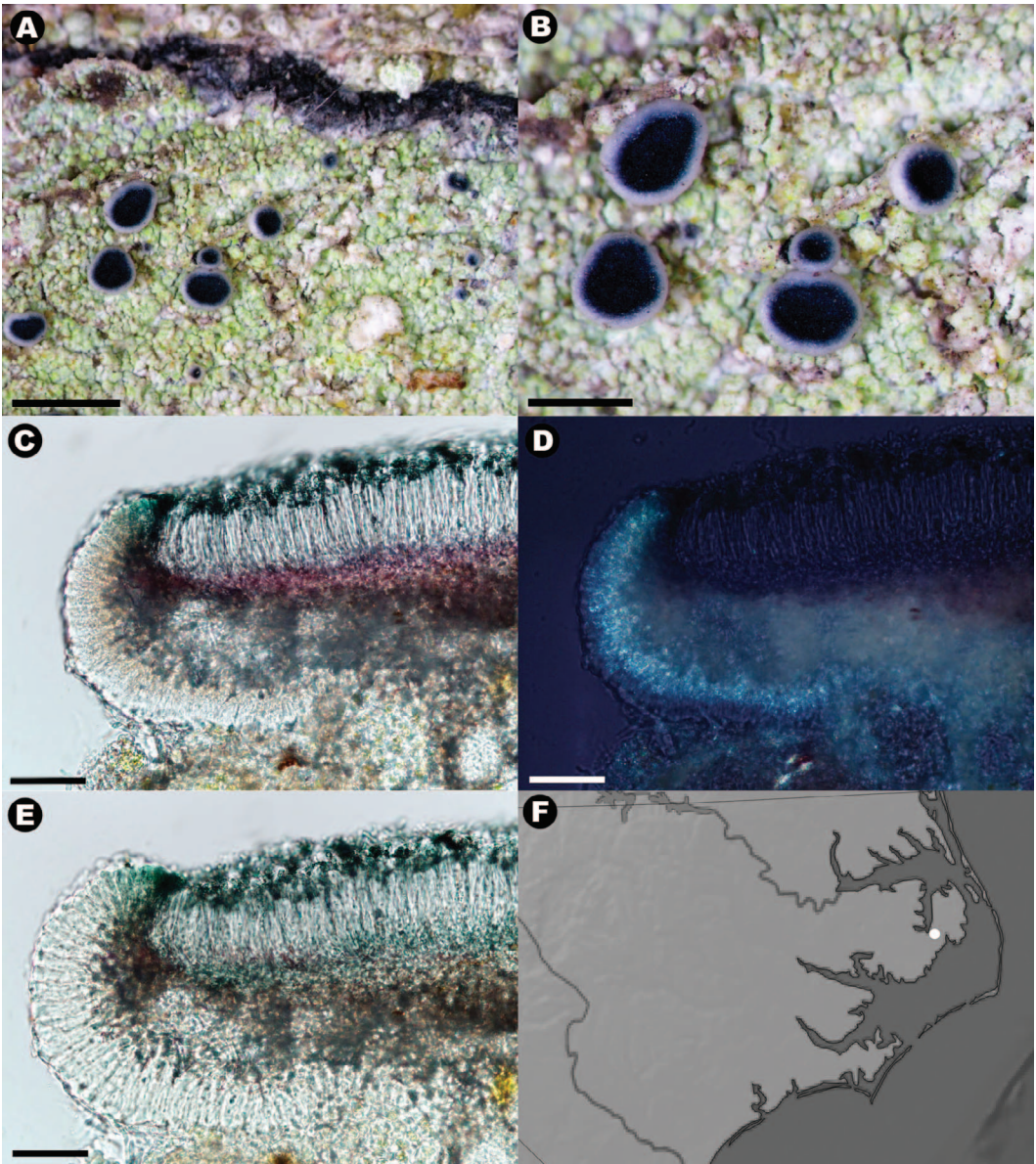


Figure 18. *Megalaria alligatorensis* morphology (A–E, from the holotype) and geographic distribution. A. Gross morphology of the thallus. B. Detail of apothecia. C–E. Transverse section in water (C), in water under polarized light (D), and after treatment in K (E). F. Geographic distribution of *M. alligatorensis*. Scale bars = 1.0 mm in A, 0.5 mm in B, and 50 μ m C–E.

single, broadly circumscribed genus pending further study with molecular data. To date, such studies have not been undertaken, and thus the new species is assigned to *Megalaria* in a broad sense. Among the species of *Megalaria* s.l., *M. alligatorensis* is distinctive on account of its

chemistry (atranorin, zeorin, and fumarprotocetraric acid), relatively smooth esorediate thallus, apothecial pigmentation, including stark white margins, and small ascospores. It is most similar to *M. albocincta* (Degel.) Tønsberg, a species that was originally described from the Azores

(Degelius 1941a) and subsequently reported from a single North American site in a high-elevation southern Appalachian spruce–fir forest (Degelius 1941b). Indeed, both *M. albocincta* and *M. alligatorensis* have similar apothecial pigmentation, esorediate thalli, and *M. albocincta* occasionally produces fumarprotocetraric acid as an accessory to atranorin and zeorin (while fumarprotocetraric acid was present in both specimens of *M. alligatorensis* examined) (Ekman and Tønsberg 1996). Nonetheless, *M. alligatorensis* can be distinguished from *M. albocincta* by its smaller ascospores ($12\text{--}14 \times 3.8\text{--}5.5 \mu\text{m}$ in *M. alligatorensis* vs. $[13\text{--}]15\text{--}17 \times 6.5\text{--}8.5 \mu\text{m}$ in *M. albocincta* *fide* Degelius [1941a]), the brown pigment in the hypothecium in *M. alligatorensis*, and by an apparent preference for hardwood substrates in *M. alligatorensis* rather than the coniferous substrates *M. albocincta* occurs on. It should be noted that Schumm and Aptroot (2013: 289) illustrated and described a sorediate specimen from Terceira in the Azores under the name *M. albocincta*. Although geographically proximal to the type locality of *M. albocincta*, the material differs from the published accounts of *M. albocincta* in having a sorediate thallus.

Megalaria anaglyptica (Kremp.) Fryday and Lendemer is a Brazilian esorediate species that also produces atranorin, zeorin, and fumarprotocetraric acid (Kalb 2007). That species is easily distinguished from *M. alligatorensis* by its thick, lumpy, granular thallus, an absence of purple pigment in the hypothecium, and by its larger ascospores ($17\text{--}22 \times 4\text{--}6 \mu\text{m}$ *fide* Kalb 2007). In treating *M. anaglyptica*, Kalb (2007) also mentioned the existence of material from Minas Gerais in Brazil that differed from the type in having smaller granules and smaller ascospores. Further study of that material should be undertaken in conjunction with study of *M. alligatorensis*.

Additional specimen examined. – Same locality as for the type, 19 March 2014, on *Magnolia virginiana*, J.C. Lendemer et al. 43134 (NY).

***Minutoexcipula miniatoexcipula* R.C.**

Harris & Lendemer sp. nov.

Mycobank #815,468

Figures 19 and 20

Diagnosis. – Differing from all known species of *Minutoexcipula* D. Hawksw. & V. Atienza in

the dark orange–red–pigmented exciple and nonseptate conidia.

TYPE: USA, NORTH CAROLINA. Washington Co.: Bull Neck Swamp, Deep Creek Rd., north of junction with Bear Lane, $35^{\circ}56'56''\text{N}$ $76^{\circ}24'02''\text{W}$, 1 ft., swamp forest with *Chamaecyparis*, *Taxodium*, and mixed hardwoods (*Acer*, *Magnolia virginiana*, *Persea*) with *Lyonia-Ilex glabra* understory, 23 March 2013, on *Pertusaria epixantha* on large *Magnolia virginiana*, J.C. Lendemer et al. 36395 (NY!, holotype).

Description. – *Conidiomata* sporodochia-like, on thallus and warts of *Pertusaria epixantha*, not usually causing any evident damage, but occasionally occurring on hosts where the thallus has become degraded, presumably by the infection, black, discoid, slightly constricted at base, 50- to $150\text{--}\mu\text{m}$ across, ca. $50\text{--}\mu\text{m}$ tall; exciple pigmented orange red, $\pm$ unchanged in KOH, ca. $10\text{--}\mu\text{m}$ thick, composed of relatively few $\pm$ rounded cells; *conidiophores* 7- to $14\text{--}\mu\text{m}$ long; *conidia* dark brown, obpyriform with one end truncate, $4.7\text{--}5.3\text{--}5.8 \times 3.0\text{--}3.3\text{--}4.0 \mu\text{m}$.

Etymology. – The species is named for the distinctive orange red color of the exciple, “miniatus” plus “excipulum.”

Ecology and distribution. – *Minutoexcipula miniatoexcipula* is currently known from two disjunct clusters of populations in inland swamp forests of the MACP in North and South Carolina (Figure 19F). This disjunct distribution does not appear to be an artifact of collection bias, as our inventory did not detect the species in the intervening area. The presence of the species in these two areas may reflect the availability of large areas of relatively high-quality intact habitat found there. To date, all of the known populations have been found on the thallus and warts of *Pertusaria epixantha*, which is widespread and common in southeastern North America, including in the area between the two known clusters of populations of *M. miniatoexcipula*. In several cases, it was not possible to determine the host lichen with certainty, because the thallus was small, sterile, or highly degraded by the infection of the *Minutoexcipula*. Nonetheless, in all such cases, the host appeared to be *P. epixantha* and not another species of *Pertusaria*.

Discussion. – The red color of the exciple and the nonseptate conidia found in the new species have not been reported for the genus *Minutoex-*

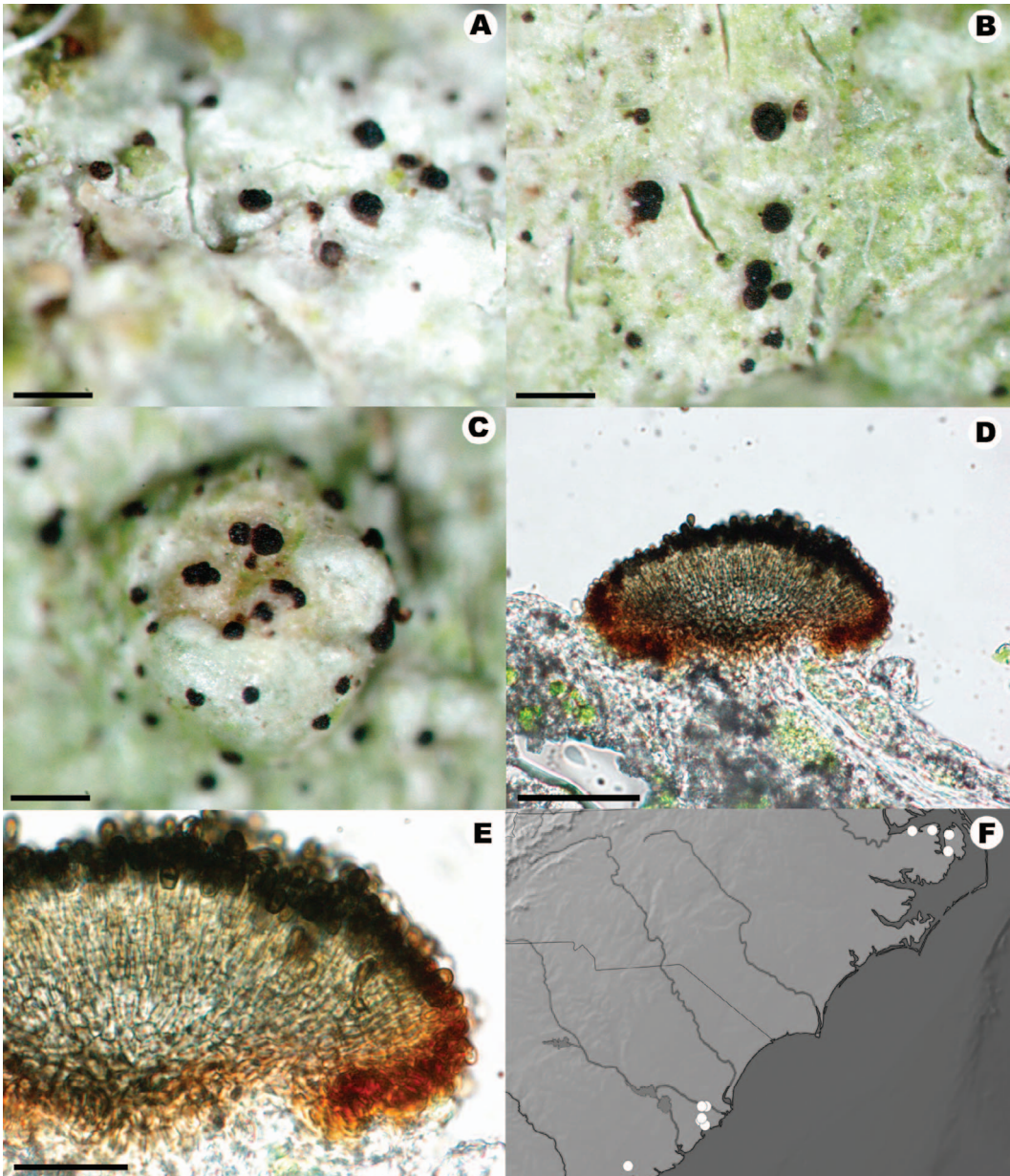


Figure 19. Morphology and distribution of *Minutoexcipula miniatorexipula* (all micrographs from the holotype). A–C. Detail of sporodochia on thallus (A and B) and ascomatal warts (C) of *Pertusaria epixantha*. D and E. Transverse sections of a sporodochium mounted in water. F. Geographic distribution of *M. miniatorexipula*. Scale bars = 0.25 mm in A–C, 50 μ m in D, and 20 μ m in E.

cipula (Atienza and Hawksworth 1994, Diederich 2003). Nonetheless, the elongate, septate conidiophores, presence of an exciple, and occurrence on *Pertusaria* indicate that it should be included in *Minutoexcipula*. While we cannot

discount the possibility that the red coloration of the exciple is a result of an interaction with the host, the species is otherwise easily distinguished by the small, nonseptate conidia. With the description of the new species here, there

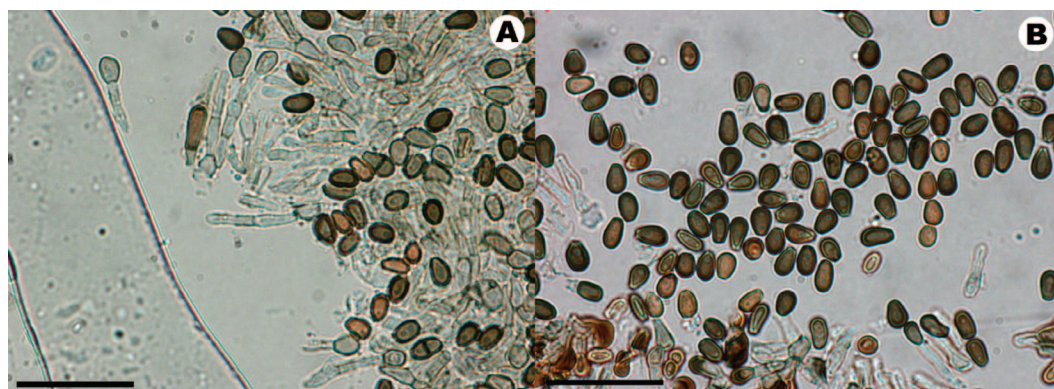


Figure 20. A, conidiophores of *Minutoexcipula miniatoexcipula*. B, Conidia of *M. miniatoexcipula*. Scale bars = 20 μ m. Both images from the holotype.

are three species of *Minutoexcipula* that occur on members of the genus *Pertusaria*. However, in our experience, they are confined to separate, albeit morphologically similar, host species in eastern North America. While *M. miniatoexcipula* is a parasite of *P. epixantha*, *M. mariana* is parasitic on *P. pustulata* and *M. tuckerae* is parasitic on *P. texana*.

Additional specimens examined. – **USA, NORTH CAROLINA. Dare Co.:** Alligator River National Wildlife Refuge, west of Buffalo City Rd., 1.2 mi south of US 64, 12 December 2012, on *P. epixantha* on *Acer*, W.R. Buck 60160 (NY); Alligator River National Wildlife Refuge, west of Whipping Creek Rd. 0.5 mi north of junction with Chip Rd., 23 March 2014, on *P. epixantha* on dead *Lyonia* branch, W.R. Buck 63061 (NY), on *P. epixantha* on *Ilex*, R.C. Harris 60264 (NY). Tyrrell Co.: Alligator River Game Land, Middle Rd. 0–0.25 mi northeast of US 64, 1.8 mi northwest of Alligator, 22 March 2014, on *P. epixantha* on *Acer*, W.R. Buck 63049 (NY), R.C. Harris 60240A (NY). **USA, SOUTH CAROLINA. Berkeley Co.:** Francis Marion National Forest, vicinity of Pitch Landing at terminus of FS 192, 6 December 2013, on *P. epixantha* on fallen branch, W.R. Buck 62099 (NY); Francis Marion National Forest, FS 204F, 0.25 mi south of McConnel's Landing, 3 December 2013, on *Pertusaria* sp. on *Quercus*, J.C. Lendemer et al. 40946 (NY). Charleston Co.: Francis Marion National Forest, Buck Hall Recreation Area, Palmetto Trailhead at terminus of FS 242, 1 December 2013, on *P. epixantha* on *Quercus*, W.R. Buck 61724 (NY); Francis Marion National Forest, Wambaw

Swamp, east of Elden Rd./ FS C-10-217, 0.3 mi south of junction with Victor Lincoln Rd./ FS C-10-154, 1 December 2013, on *P. epixantha* on *Acer*, W.R. Buck 61807 (NY); Francis Marion National Forest, Wambaw Swamp Wilderness, Wambaw Swamp, at bridge on Elden Rd./FS C-10-217, 0.4 mi north of junction with FS 217A, 1 December 2013, on *Pertusaria* sp. on *Acer*, J.C. Lendemer et al. 40270 (NY). Colleton Co.: Donnelley Wildlife Management Area, 0.2 mi southwest of Main Rd., 0.7 mi north of junction with Blocker Run Rd., 18 December 2013, on *P. epixantha* on *Nyssa*, J.C. Lendemer et al. 41710 (NY).

***Trichosphaerella buckii* R.C. Harris & Lendemer sp. nov.**
Mycobank #815,469

Figure 21

Diagnosis. – *Trichosphaerella* E. Bommer, M. Rousseau, and Sacc. with perithecia immersed in the thallus of *Punctelia rudecta*. Perithecia conical, brown, with unbranched septae around the ostiole. Ascospores breaking into 16 part spores. Part spores colorless, tetrahedral, with papillae at the apices.

TYPE: USA, NORTH CAROLINA. Tyrrell Co.: Alligator River Game Land, Middle Rd. 0.025 mi northeast of US 64, 1.8 mi northwest of Alligator, 35°55'34"N, 76°08'05"W, 0 m, mixed hardwood (*Nyssa*, *Acer*, *Magnolia virginiana*)–*Taxodium* swamp forest, on *Punctelia rudecta* on trunk of *Acer*, 22 March 2014, W.R. Buck 63057 (NY!, holotype).

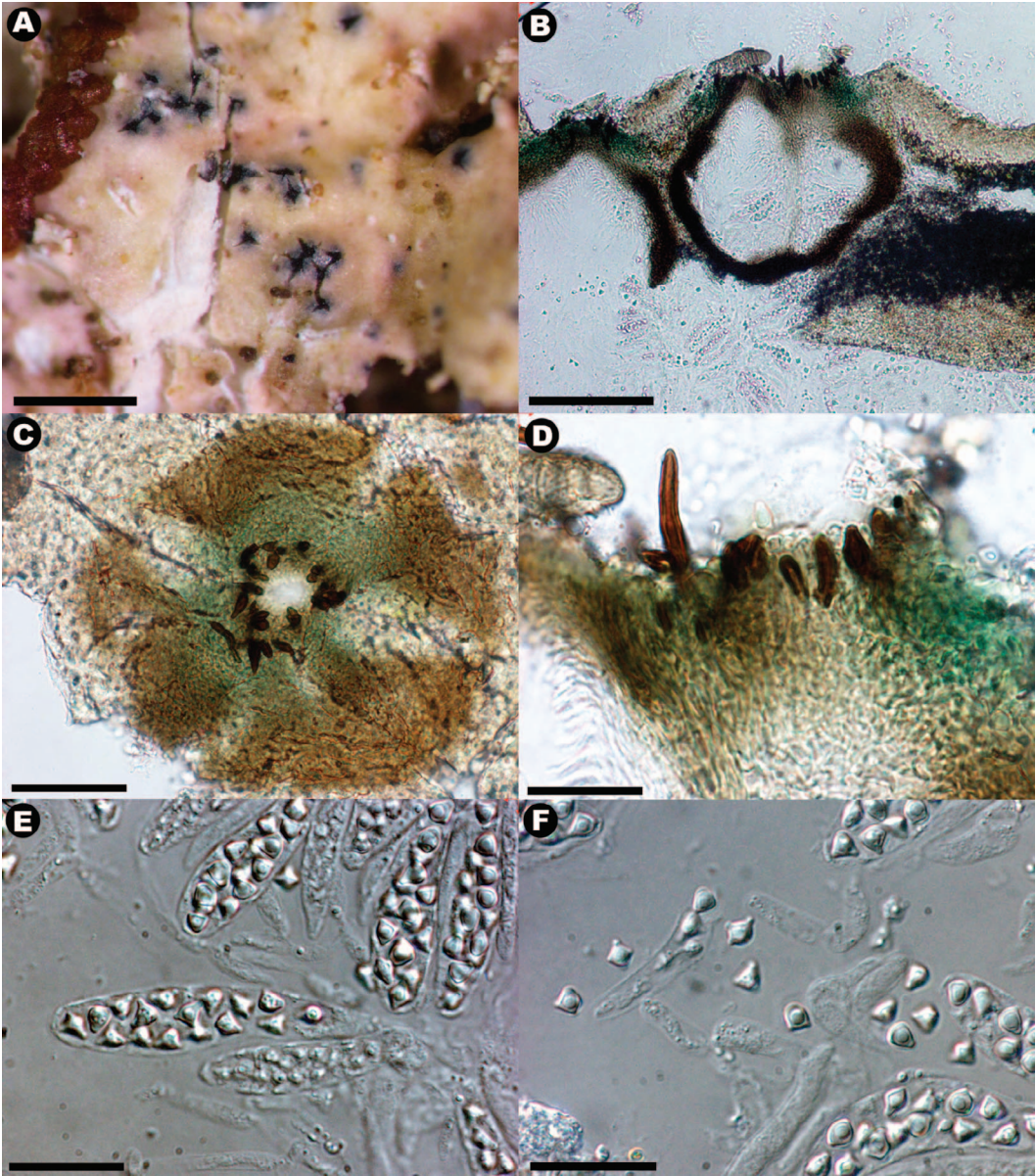


Figure 21. *Trichosphaerella buckii* (all from the holotype). A. Detail of infection with emergent perithecia. B. Transverse section of perithecium in water. C. Mount of perithecium in water viewed from above. D. Detail of ostiolar setae in water. E. Asci and intact ascospores. F. Part-spores. Scale bars = 0.5 mm in A, 100 µm in B and C, and 20 µm in D–F.

Description. – *Perithecia* parasitic or saprophytic(?), immersed in moribund thallus of *Punctelia rudecta*, conical, ca. 0.1- to 0.2-mm across, 0.8- to 0.17-mm tall, with erumpent apex; *perithecial wall* prosoplectenchymatous, entire, olivaceous, greenish around the ostiole, ca. 15-

µm thick; *erumpent ostiolar region* with brown, unbranched setae, ca. 15–25 × 4–4.5 µm long; *ostiolar region* periphysate; *paraphyses* sparse, thin walled, unbranched, ca. 2.5- to 3.0-µm wide; *hymenial gel* Γ⁺. *Asci* cylindrical, thin walled, without tholus, Γ⁺, 50–65 × 11–13 µm, with 16

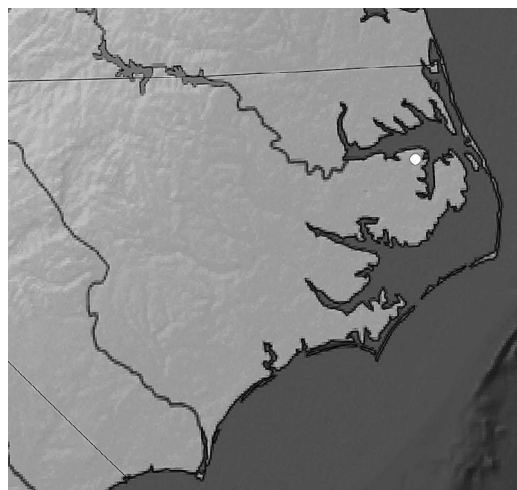


Figure 22. Geographic distribution of *Trichosphaerella buckii*.

part spores; *part spores* hyaline, tetrahedral with papillate apices, 4- to 6- μ m across (including papillae). *Pycnidia* not seen.

Etymology. – The epithet honors William R. Buck (b. 1950), astute collector of minute lichens and lichenicolous fungi who contributed greatly to our inventory of the DRBH and the MACP. Many species have been elevated from obscurity via formal scientific description as a result of collections he has made.

Ecology and distribution. – *Trichosphaerella buckii* is known only from the type collection, found growing on *Punctelia rudecta* in the Coastal Plain of eastern North Carolina (Figure 22). Considering that the host is common and widespread, both in the Coastal Plain and, more generally, throughout temperate eastern North America, it is possible that new species may prove to be more widespread.

Discussion. – *Trichosphaerella buckii* is easily recognized by the immersed, erumpent, setose perithecia, and the asci with 16 apically papillate tetrahedral part spores. This is the first report of a lichenicolous species of *Trichosphaerella*. The genus is a member of the Niessliaceae, distinguished from *Niesslia* Auersw. by the eight initial ascospores separating into 16 part spores (Samuels and Barr 1997, Rossman et al. 1999). Although other species placed in the genus are saprophytic, *T. goniospora* Döbbele et al. (2015) with similar tetrahedral part spores was recently described from a liverwort. *Niesslia tetrahedrospora* Etayo, which was described from the lichen *Dichosporidium nigrocinctum* (Ehrenb.) G. Thor by Etayo (2002) has similar part spores and could also be placed in *Trichosphaerella*. Both *N. tetrahedrospora* and *T. goniospora* differ from the new taxon in host, in having superficial perithecia, and in lacking papillae on the spore apices.

APPENDIX II: Checklist of the Lichens and Allied Fungi of the Dare Regional Biodiversity Hotspot (DRBH)

The checklist presented below is arranged alphabetically by genus and species. Taxa not identified to species are largely excluded from the list, as are unpublished names of new species for which descriptions are currently in preparation. When partially identified taxa, or unpublished names, are included in the list, it is because the taxon is common enough to be frequently encountered in the study area. Throughout the list, lichenicolous fungi are denoted by an asterisk (*) before the name, and nonlichenized fungi that are treated with lichens are denoted with a plus symbol (+) before the name. Taxonomy and taxonomic authorities largely follow Esslinger (2014), and deviations from that work reflect the opinions of the authors.

**Abrothallus parmotrematis* Diederich
Acanthothecis leucoxanthoides Lendemer
Acanthothecis mosquitensis (Tuck.) E. A. Tripp
 & Lendemer
Acanthothecis paucispora Lendemer & R.C.
 Harris
Acrocordia gemmata (Ach.) A. Massal.
Aggyrium rufum (Pers.) Fr.
Amandinea langloisii Marbach
Amandinea milliaria (Tuck.) P. May & Sheard
Amandinea polyspora (Willey) E. Lay & P. May

Amandinea punctata (Hoffm.) Coppins &
 Scheid.
Anaptychia palmulata (Michx.) Vain.
Anisomeridium anislobum (Müll. Arg.) Apt-
 root
Anisomeridium biforme (Borrer) R.C. Harris
Anisomeridium biformoides R.C. Harris
Anisomeridium polypori (Ellis & Everh.) M. E.
 Barr
Anthracothecium nanum (Zahlbr.) R.C. Harris
Anzia colpodes (Ach.) Stizenb.

- Anzia ornata* (Zahlbr.) Asahina
 **Arthonia agelastica* R.C. Harris & Lendemer
Arthonia albobirescens Nyl.
Arthonia anglica Coppins
Arthonia cinnabarina (DC.) Wallr.
Arthonia hodgesii Lendemer & R.C. Harris
Arthonia interveniens Nyl.
 +*Arthonia quintaria* Nyl.
Arthonia ruana A. Massal.
Arthonia rubella (Fée) Nyl.
 **Arthonia stevensoniana* R.C. Harris & Lendemer
Arthonia susa R.C. Harris & Lendemer
 +*Arthopyrenia cinchonae* (Ach.) Müll. Arg.
 +*Arthopyrenia taxodii* R.C. Harris
Asterothyrium decipiens (Rehm) R. Sant.
Bacidia diffracta S. Ekman
Bacidia helicospira S. Ekman
Bacidia heterochroa (Müll. Arg.) Zahlbr.
Bacidia schweinitzii (Fr. ex Tuck.) A. Schneid.
Bacidina sp. This is a common species in the DRBH and MACP that occurs on the bark of hardwoods and can be recognized by its pale-brownish apothecia that lack internal pigments, lack POL⁺ crystals, and the absence of secondary chemistry.
Bacidina crystallifera S. Ekman
Bacidina egenula (Nyl.) Vězda
Bacidina varia S. Ekman
Bactrospora brevispora R.C. Harris
Bactrospora carolinensis (Ellis & Everh.) R.C. Harris
Bactrospora lamprospora (Nyl.) Lendemer
Bathelium carolinianum (Tuck.) R.C. Harris
Brigantiaea leucoxantha (Spreng.) R. Sant. & Hafellner
Buellia curtisii (Tuck.) Imshaug
Buellia elizae (Tuck.) Tuck.
Buellia imshaugiana R.C. Harris
Buellia stillingiana J. Steiner
Buellia vernicoma (Tuck.) Tuck.
Buellia wheeleri R.C. Harris
 **Buelliella minimula* (Tuck.) Fink
 **Buelliella tryptethelii* (Tuck.) Fink
Bulbothrix isidiza (Nyl.) Hale
Bulbothrix scortella (Nyl.) Hale
Byssoloma leucoblepharum (Nyl.) Vain.
Byssoloma meadii (Tuck.) S. Ekman
Caloplaca camptidia (Tuck.) Zahlbr.
Caloplaca feracissima H. Magn.
Caloplaca flavorubescens (With.) J.R. Laundon
Candelaria concolor (Dicks.) Stein
Candelariella xanthostigmoides (Müll. Arg.) R.W. Rogers
Canoparmelia amazonica (Nyl.) Elix & Hale
Canoparmelia caroliniana (Nyl.) Elix & Hale
Catinaria atropurpurea (Schaer.) Vězda & Poelt
Chaenotheca hygrophila Tibell
Chaenothecopsis debilis (Sm.) Tibell
Chaenothecopsis nana Tibell
Chaenothecopsis pusilla (Ach.) A.F.W. Schmidt
Chaenothecopsis pusiola (Ach.) Vain.
Chrysothrix chamaecyparicola Lendemer
Chrysothrix xanthina (Vain.) Kalb
Cladonia atlantica A. Evans
Cladonia beaumontii (Tuck.) Vain.
Cladonia caespiticia (Pers.) Flörke
Cladonia didyma var. *vulcanica* (Zoll. & Moritz) Vain.
Cladonia evansii Abbayes
Cladonia incrassata Flörke
Cladonia leporina Fr.
Cladonia macilenta var. *bacillaris* (Genth) Schaer.
Cladonia ochrochlora Flörke
Cladonia parasitica (Hoffm.) Hoffm.
Cladonia peziziformis (With.) J.R. Laundon
Cladonia polycarpia G. Merr.
Cladonia ramulosa (With.) J.R. Laundon
Cladonia rappii A. Evans
Cladonia santensis Tuck.
Cladonia subradiata (Vain.) Sandst.
Cladonia subtenuis (Abbayes) Mattick
Coccocarpia erythroxyli (Spreng.) Swinsc. & Krog
Coccocarpia palmicola (Spreng.) Arv. & D.J. Galloway
Coenogonium luteum (Dicks.) Kalb & Lücking.
 Note. – This name is used here in a broad sense for a taxon that is common and widespread in the southeastern Coastal Plain, but that is strongly disjunct from the typical range of the species in northern temperate or boreal regions (see Brodo et al. 2001). Specimens referred to this species in the MACP likely belong to a separate species; however, its distinction from *C. luteum* requires extensive additional study beyond the scope of the present work.
Collema pulcellum Ach. var. *leucopeplum* (Tuck.) Degel.
Collema subflaccidum Degel.
 **Coniambigua phaeographidis* Etayo & Diederich

- Coniarthonia pyrrhula* (Nyl.) Grube
 **Cornutispora triangularis* Diederich & Etayo
Crespoa crozalsiana (Harm.) Lendemer & B.P. Hodk.
Cresponea flava (Vain.) Egea & Torrente
 **Dactylospora inquilina* (Tuck.) Hafellner
Dendriscoaulon intricatulum (Nyl.) Henssen
 **Didymocyrtis melanelixiae* (Brackel) Diederich, R.C. Harris & Etayo
Dirinaria aegialita (Ach.) B.J. Moore
Dirinaria confusa D.D. Awasthi
Dirinaria picta (Sw.) Schaer. ex Clem.
Dyplotabia afzelii (Ach.) A. Massal.
Enterographa anguinella (Nyl.) Redinger
Epigloea pleiospora Döbbeler
 **Etayoa trypethelii* (Flakus & Kukwa) Diederich & Ertz
Fellhanera bouteillei (Desm.) Vězda
Fissurina alligatorensis Lendemer & R.C. Harris
Fissurina columbina (Tuck.) Staiger
Fissurina cypressi (Müll. Arg.) Lendemer
Fissurina illiterata (R.C. Harris) Lendemer
Fissurina incrustans Fée
Fissurina insidiosa C. Knight & Mitt.
Fissurina scolecitis (Tuck.) Lendemer
Fissurina subnitidula (Tuck.) Staiger
Flavoparmelia caperata (L.) Hale
Fuscopannaria leucosticta (Tuck.) P.M. Jørg.
Gassicurtia acidobaeomyceta Marbach
Glyphis cicatricosa Ach.
Glyphis scyphulifera (Ach.) Staiger
Graphis cincta (Pers.) Aptroot
Graphis crebra Vain.
Graphis desquamescens Fée
Graphis duplicata Ach.
Graphis endoxantha Nyl.
Graphis furcata Fée
Graphis handelii Zahlbr.
Graphis intermedians Vain.
Graphis inversa R.C. Harris
Graphis lineola Ach.
Graphis pinicola Zahlbr.
Graphis scripta (L.) Ach.
Graphis striatula (Ach.) Spreng.
Graphis tenella Ach.
Graphis vittata Müll. Arg.
Gyalideopsis buckii Lücking, Sérus., & Vězda
 **Gyalideopsis floridae* Etayo & Diederich
Haematomma accolens (Stirt.) Hillmann
Haematomma americanum Staiger & Kalb
Haematomma flexuosum Hillmann
Haematomma guyanense Staiger & Kalb
Haematomma persoonii (Fée) A. Massal.
Hafellia sp. This is a species that is infrequent, but widespread, in coastal maritime forests throughout the DRBH. It does not appear to be one of the species yet known from North America; however, further study is needed before it can be described.
Heterodermia albicans (Pers.) Swinsc. & Krog
Heterodermia casarettiana (A. Massal.) Trevis.
Heterodermia crocea R.C. Harris
Heterodermia leucomelos (L.) Poelt
Heterodermia obscurata (Nyl.) Trevis.
Hypotrachyna cryptochlora (Vain.) D. Hawksw. & A. Crespo
Hypotrachyna horrescens (Taylor) Swinsc. & Krog
Hypotrachyna livida (Taylor) Hale
Hypotrachyna minarum (Vain.) Krog & Swinsc.
Hypotrachyna osseocalba (Vain.) Y.S. Park & Hale
Hypotrachyna spumosa (Asahina) Krog & Swinsc.
 **Intralichen lichenum* (Diederich) D. Hawksw. & M.S. Cole
Lecanora caesiorubella Ach. subsp. *glaucomodes* (Nyl.) Imshaug & Brodo
Lecanora chlarotera Nyl.
Lecanora cinereofusca H. Magn.
Lecanora cupressi Tuck.
Lecanora floridula Lumbsch
Lecanora hybocarpa (Tuck.) Brodo
Lecanora imshaugii Brodo
Lecanora louisianae B. de Lesd.
Lecanora nothocaesiella R.C. Harris & Lendemer
Lecanora strobilina (Spreng.) Kieff.
Lecanora subpallens Zahlbr.
Leiorreuma explicans (Fink) Lendemer
Leiorreuma sericeum (Eschw.) Staiger
Lepraria aurescens Orange & Wolesley
Lepraria finkii (B. de Lesd.) R.C. Harris
Lepraria friabilis Lendemer, K. Knudsen, & Elix
Lepraria harrisiana Lendemer
Lepraria hodkinsoniana Lendemer
Lepraria vouauxii (Hue) R.C. Harris
Leptogium austroamericanum (Malme) C.W. Dodge
Leptogium azureum (Sw.) Mont.
Leptogium corticola (Taylor) Tuck.
Leptogium cyanescens (Rabenh.) Körb.
 **Lichenochora haematommatum* R.C. Harris & Lendemer
 **Lichenocodium cargillianum* (Linds.) D. Hawksw.

- **Lichenocodium lecanorae* (Vouaux) Dyko & D. Hawksw.
 **Lichenodiplis lecanorae* (Vouaux) Dyko & D. Hawksw.
Lobaria ravenelii (Tuck.) Yoshim.
Loxospora confusa Lendemer
Maronea polyphaea H. Magn.
Mazosia carnea (Eckfeldt) Aptroot & M. Cáceres
Megalospora pachycheila (Tuck.) Sipman
Megalospora porphyritis (Tuck.) R.C. Harris
 **Melanographa tribulodes* (Tuck.) Müll. Arg.
 **Merismatium* sp. This taxon was found growing on a thallus of *Rinodina maculans* in an inland swamp. As only a single small specimen was available, we have refrained from studying it further until additional material is located.
Micarea chlorosticta (Tuck.) R.C. Harris
Micarea micrococca (Körb.) Gams ex Coppins
Micarea neostipitata Coppins & P. May
Micarea peliocarpa (Anzi) Coppins & R. Sant.
Micarea prasina Fr.
 **Minutoexcipula mariana* V. Atienza
 **Minutoexcipula miniatoexcipula* R.C. Harris & Lendemer
 **Minutoexcipula tuckerae* V. Atienza & D. Hawksw.
 **Muellerella lichenicola* (Sommerf.) D. Hawksw.
Multiclavula mucida (Fr.) R.H. Petersen
Mycocalicium subtile (Pers.) Szatala
 +*Mycoporum eschweileri* (Müll. Arg.) R.C. Harris
 +*Mycoporum lacteum* (Ach.) R.C. Harris
Myelochroa aurulenta (Tuck.) Elix & Hale
Nadvornikia sorediata R.C. Harris
 **Nectriopsis rubefaciens* (Ellis & Everh.) M.S. Cole & D. Hawksw.
Ocellularia americana Hale
Ocellularia praestans (Müll. Arg.) Hale
Ocellularia sanfordiana (Zahlbr.) Hale
Ochrolechia africana Vain.
 **Opegrapha anomea* Nyl.
Opegrapha corticola Coppins & P. James
Opegrapha varia Pers.
Opegrapha viridis (Ach.) Behlen & Desberger
Opegrapha vulgata Ach.
Pannaria lurida (Mont.) Nyl. subsp. *quercicola* P.M. Jørg.
Pannaria tavaresii P.M. Jørg.
Parmeliella pannosa (Sw.) Müll. Arg.
Parmeliopsis subambigua Gyeln.
Parmotrema dilatatum (Vain.) Hale
Parmotrema gardneri (C.W. Dodge) Sérus.
Parmotrema hypoleucinum (J. Steiner) Hale
Parmotrema hypotropum (Nyl.) Hale
Parmotrema internexum (Nyl.) Hale
Parmotrema madagascariaceum (Hue) Hale
Parmotrema mellissii (C.W. Dodge) Hale
Parmotrema neotropicum Kurok.
Parmotrema perforatum (Jacq.) A. Massal.
Parmotrema praesorediosum (Nyl.) Hale
Parmotrema rampoddense (Nyl.) Hale
Parmotrema reticulatum (Taylor) M. Choisy
Parmotrema subisidiosum (Müll. Arg.) Hale
Parmotrema submarginale (Michx.) DePriest & B. Hale
Parmotrema subrigidum Egan
Parmotrema tinctorum (Nyl.) Hale
Parmotrema ultralucens (Krog) Hale
Parmotrema xanthinum (Müll. Arg.) Hale
Peltigera neopolydactyla (Gyeln.) Gyeln.
Pertusaria epixantha R.C. Harris
Pertusaria neoscotica I.M. Lamb
Pertusaria obruta R.C. Harris
Pertusaria paratuberculifera Dibben
Pertusaria propinqua Müll. Arg.
Pertusaria pustulata (Ach.) Duby
Pertusaria sinusmexicani Dibben
Pertusaria subpertusa Brodo
Pertusaria tetrathalamia (Fée) Nyl.
Pertusaria texana Müll. Arg.
 +*Phaeocalicium polyporaenum* (Nyl.) Tibell
Phaeographis brasiliensis (A. Massal.) Kalb & Matthes-Leicht
Phaeographis erumpens (Nyl.) Müll. Arg.
Phaeographis inusta (Ach.) Müll. Arg.
Phaeographis lobata (Eschw.) Müll. Arg.
Phaeographis oricola Lendemer & R.C. Harris
Phaeophyscia pusilloides (Zahlbr.) Essl.
Phaeophyscia rubropulchra (Degel.) Essl.
Phaeophyscia squarrosa Kashiw.
 **Phaeosporobolus alpinus* R. Sant., Alstrup, & D. Hawksw.
Phlyctis boliviensis Nyl.
Phyllopsora confusa Swinsc. & Krog
Phyllopsora parvifolia (Pers.) Müll. Arg.
Physcia americana G. Merr.
Physcia atrostriata Moberg
Physcia millegrana Degel.
Physcia pumilior R.C. Harris
Physcia sorediosa (Vain.) Lynge
Piccolia nannaria (Tuck.) Lendemer & Beeching
Placynthiella dasaea (Stirt.) Tønsberg
Placynthiella icmalea (Ach.) Coppins & P. James

- Polymeridium proponens* (Nyl.) R.C. Harris
Polymeridium quinqueseptatum (Nyl.) R.C. Harris
Polymeridium subcinereum (Nyl.) R.C. Harris
Porina heterospora (Fink) R.C. Harris
Porina scabrada R.C. Harris
**Pronectria subimperspicua* (Speg.) Lowen
Protoparmelia isidiata Diederich, Aptroot & Srus.
Pseudosagedia cestrensis (Tuck.) R.C. Harris
Pseudosagedia isidiata (R.C. Harris) R.C. Harris
Pseudosagedia raphidosperma (Mll. Arg.) R.C. Harris
Psoroglaena dictyospora (Orange) H. Harada
Punctelia missouriensis G. Wilh. & Ladd
Punctelia rudecta (Ach.) Krog
Pyrenula anomala (Ach.) R.C. Harris
Pyrenula aspistea Ach.
Pyrenula citrififormis R.C. Harris
Pyrenula cruenta (Mont.) Vain.
Pyrenula leucostoma Ach.
Pyrenula mamillana (Ach.) Trevis.
Pyrenula microcarpa Mll. Arg.
Pyrenula microtheca R.C. Harris
Pyrenula pseudobufonia (Rehm) R.C. Harris
Pyrenula punctella (Nyl.) Trevis.
Pyrenula ravenelii (Tuck.) R.C. Harris
Pyrenula santensis (Nyl.) Mll. Arg.
Pyrgillus javanicus Nyl.
Pyrrhospora sp. This species, widespread in the southeastern Coastal Plain, has been confused with *Pyrrhospora querneae* (Dicks.) Krb. when collected. It differs from that species in several respects and will be described in a future publication.
Pyrrhospora varians (Ach.) R.C. Harris
Pyxine albobirens (G. Mey.) Aptroot
Pyxine caesiopruinosa (Nyl.) Imshaug
Pyxine sorediata (Ach.) Mont.
Pyxine subcinerea Stirt.
Ramalina complanata (Sw.) Ach.
Ramalina culbertsoniorum LaGreca
Ramalina stenospora Mll. Arg.
Ramalina willeyi R. Howe
Ramboldia russula (Ach.) Kalb, Lumbsch & Elix
Ramonia microspora Vzda
Rinodina dolichospora Malme
Rinodina maculans Mll. Arg.
Rinodina papillata H. Magn.
Ropalospora viridis (Tnsberg) Tnsberg
**Roselliniopsis tropica* Matzer & R. Sant.
Sarcographa tricola (Ach.) Mll. Arg.
Schismatomma rappii (Zahlbr.) R.C. Harris
Schrakia sp.? This is a very unusual species that does not appear to be lichenized, but nonetheless would easily be confused with members of the genus *Melaspilea* on account of its brown, two-celled ascospores. It typically occurs on the bark of trees in swamp forests and can easily be recognized in the field by the presence of small, brownish-black apothecia with distinctly red pruinose margins. We include the species here because it is not uncommon and we have been unable to locate a name for it.
Segestria leptalea (Durieu & Mont.) R.C. Harris
**Skyttea lecanorae* Diederich & Etayo
**Sphinctrina tubiformis* A. Massal.
Sticta carolinensis T. McDonald
Sticta deyana Lendemer & Goffinet
Strigula americana R.C. Harris
Strigula viridiseda (Nyl.) R.C. Harris
**Taeniolella delicata* M.S. Christ. & D. Hawksw.
Teloschistes chrysophthalmus (L.) Tuck.
Tephromela atra (Huds.) Hafellner
Thalloloma cf. *cinnabarinum* (Fe) Staiger
Thalloloma hypoleptum (Nyl.) Staiger
Thelopsis rubella Nyl.
Thelotrema adjectum Nyl.
Thelotrema defectum R.C. Harris
Thelotrema dilatatum (Mll. Arg.) Hale
Thelotrema lathraeum Tuck.
Thelotrema monospermum R.C. Harris
Thelotrema subtile Tuck.
Topelia aperiens P. M. Jrg. & Vzda
Trapeliopsis flexuosa (Fr.) Coppins & P. James
**Tremella parmeliarum* Diederich
**Tremella harrisii* Diederich
**Tremella pertusariae* Diederich
**Tremella phaeographidis* Diederich, Coppins & Bandoni
**Tremella* sp. This taxon was found growing on a thallus of *Lecanora louisianae*. Because only one small specimen was available, we have refrained from studying it further until additional material is located.
**Trichosphaerella buckii* R.C. Harris & Lendemer
Trichothelium americanum Lendemer
Trypethelium tropicum (Ach.) Mll. Arg.
Trypethelium virens Tuck.
Tuckermanella fendleri (Nyl.) Essl.
Usnea baileyi (Stirt.) Zahlbr.
Usnea endochrysea Stirt.
Usnea evansii Motyka
Usnea mutabilis Stirt.

Usnea pensylvanica Motyka

Usnea strigosa (Ach.) Eaton

Usnea subscabrosa Motyka

Usnea trichodea Ach.

Variolaria amara Ach.

Variolaria commutata (Mull. Arg.) ined.
($\equiv$ *Pertusaria commutata* Mull. Arg.)

Variolaria hypothamnolica (Dibben) ined.
($\equiv$ *Pertusaria hypothamnolica* Dibben)

Variolaria multipunctoides (Dibben) Lendemer, B.P. Hodk., & R.C. Harris

Variolaria ophthalmiza (Nyl.) Darb.

Variolaria pustulata (Brodo & W.L. Culb.) Lendemer, B.P. Hodk., & R.C. Harris

Variolaria trachythallina (Erichsen) Lendemer, B.P. Hodk., & R.C. Harris

Vezdaea leprosa (P. James) Vězda

**Vouauxiella lichenicola* (Linds.) Petr. & Syd.

Xyleborus nigricans R.C. Harris & Lendemer

APPENDIX III: KEYS TO THE LICHENS, LICHENOLCOUS FUNGI AND ALLIED FUNGI OF THE DARE REGIONAL BIODIVERSITY HOTSPOT

Below we present keys to the lichens, lichenicolous fungi and allied fungi that occur in the DRBH. The keys are arranged with a main "Key to Keys" followed by subsequent smaller keys. Note that taxa included in brackets have not yet been found in the study area, but are included either to broaden the use of the keys or because there is a high chance that they occur in the DRBH. Terminology has been simplified as much as possible. We suggest that the reader refer to the introductory material and glossary of Brodo et al. (2001) for questions relating to the meaning of a given technical term.

KEY TO KEYS

1. Fungi occurring on the thalli of other lichens **Key 1. Lichenicolous Fungi**
1. Fungi not on the thalli of other lichens 2
 2. Fruiting body resembling white, fleshy clubs; fungus a basidiomycete
..... ***Multiclavula mucida* (Fr.) R. H. Petersen**
 2. Fruiting body not resembling white, fleshy clubs; fungus not a basidiomycete 3
 3. Ascomata resembling tiny black or brown pins **Key 2. Calicioid Fungi**
 3. Ascomata not as above 4
 4. Thallus foliose, fruticose or squamulose (macrolichens) 5
 5. Thallus foliose 6
 6. Photobiont a cyanobacterium, sometimes restricted to cephalodia with the primary photobiont being a green alga (all species rare or extirpated)
..... **Key 3. Foliose Cyanolichens**
 6. Photobiont a green alga, no cyanobacteria present ... **Key 4. Foliose Chlorolichens**
 5. Thallus fruticose or large squamulose 7
 7. Thallus large squamulose or dimorphic with primary thallus of squamules and secondary thallus of hollow podetia; *Cladonia/Cladina* **Key 5. Cladoniaceae**
 7. Thallus not large squamulose or dimorphic, always fruticose; not *Cladonia/Cladina* **Key 6. Fruticose Macrolichens**
 4. Thallus crustose 8
 8. Thallus on leaves **Key 7. Follicolous Lichens**
 8. Thallus on other substrates 9
 9. Thallus with lichenized diaspores (e.g., isidia, soredia) or specialized conidium bearing structures (i.e., hyphophores or stalked pycnidia), apothecia/perithecia not typically present **Key 8. Typically Asexually Reproducing Crustose Lichens**
 9. Thallus without lichenized diaspores or specialized conidium bearing structures .. 10
 10. Fruiting body a perithecium **Key 9. Crustose Pyrenolichens**
 10. Fruiting body an apothecium 11
 11. Ascospores colorless
..... **Key 10. Crustose Apotheciate Lichens with Hyaline Spores**
 11. Ascospores brown
..... **Key 11. Crustose Apotheciate Lichens with Brown Spores**

KEY 1. LICHENICOLOUS FUNGI

1. Spores produced in asci in disciform, lirelliform or flask shaped structures 2

2. Ascomata disk-like (apothecioid) or lirelliform (if hemispherical apothecioid but without asci, see *Tremella*) 3

3. Spores soon brown, simple or 1-septate 4

4. Ascomata with short stalk; spores simple, citriform (lemon-shaped), coarsely ridged *Sphinctrina tubiformis* A. Massal

4. Ascomata not stalked; spores 1-septate 5

5. Ascomata lirelliform; on *Pyrenula cruenta* *Melanographa tribulodes* (Tuck.) Müll. Arg.

5. Ascomata apothecioid; on other hosts 6

6. On thallus of *Parmotrema subrigidum*; epihymenium K+ green *Abrothallus parmotremae* Diederich

6. On warts and thallus of *Pertusaria* or *Bathelium carolinianum* 7

7. On *Bathelium carolinianum*; spores 16–19 × 8–11.5 µm *Buelliella trypethelii* (Tuck.) Fink

7. On *Pertusaria* 8

8. Asci with I+ blue cap; spores 12–15 × 6–8.5 µm; on *Pertusaria paratuberculifera* *Dactylospora inquilina* (Tuck.) Hafellner

8. Asci without I+ cap; spores 15–18 × 6–8 µm on *Pertusaria tetrathalamia* *Buelliella minimula* (Tuck.) Fink

3. Spores colorless (may become brown with age), simple to 3-septate 9

9. Ascomata dark, K– 10

10. Spores simple 11

11. On thallus of *Lecanora floridula* and *L. louisianae*; ascomata with marginal hairs; asci 8-spored, ellipsoid, 7–9 × 3–3.5 µm *Skyttea lecanorae* Diederich & Etayo

11. On thallus of *Parmotrema submarginale* & *P. subrigidum*; ascomata without marginal hairs; asci multisporeous; spores ± globose to broadly ellipsoid *Gyalideopsis floridae* Etayo & Diederich

10. Spores 1–3-septate 12

12. Spores 1-septate 13

13. Ascomata not stalked, not mazaedial; on *Haematomma accolens* or *Pyrenula cruenta* 14

14. Growing in hymenium of *Haematomma accolens*; ascomata blotchy, irregularly sharp *Arthonia stevensoniana* R.C. Harris & Lendemer

14. Growing on thallus surface of *Pyrenula cruenta*; ascomata lirelliform *Melanographa tribulodes* (Tuck.) Müll. Arg.

13. Ascomata with short stalk, mazaedial; on apothecia and thallus of *Lecanora caesiorubella* ssp. *glaucomodes*, *L. louisianae* and *L. subpallens* [*Chaenothecopsis kalbii* Tibell & K. Ryman]

12. Spores 2–3-septate 15

15. On thallus of *Lecanora louisianae*; spores 2(–3)-septate, 13–16 × 5–7.5 µm *Arthonia agelastica* R.C. Harris & Lendemer

15. On *Pertusaria*; spores 3-septate, 17–26 × 6.5–9 µm *Opegrapha anomaea* Nyl.

9. Ascomata orange, KOH+ purple or whitish to pinkish 16

16. Apothecia orange, K+ red; spores 3-septate, macrocephalic, 12–15 × 4–7 µm; on *Graphis lineola* *Arthonia hodgesii* Lendemer & R.C. Harris

16. Apothecia whitish to pinkish; margin concolorous or paler than disk; epihymenium and exciple filled with small POL+ crystals; spores needle shaped; over thallus of *Trypethelium tropicum* *Bacidia crystallifera* Ekman

2. Ascomata flask shaped (perithecioid); interascal hyphae absent or indistinct 17

17. Spores brown 18

18. Asci multisporeous; spores 1-septate; on various crustose lichens (incl. *Buelliella curtisii*, *Lecanora strobilina*, *Pertusaria epixantha* and *P. obruta*) *Muellerella lichenicola* (Sommerf.) D. Hawksw.

18. Asci 8-spored 19

19. Ascospores simple; on apothecia and thallus of *Ochrolechia africana* *Roselliniopsis tropica* Matzer & R. Sant.

19.	Ascospores submuriform; on <i>Rinodina maculans</i>	<i>Merismatium sp.</i>	
17.	Spores colorless or pale brownish (may turn dark brown in age), 1-septate		20
20.	Perithecia pink, orangish or reddish		21
21.	Perithecia immersed in thallus of <i>Punctelia rudecta</i> ; wall orangish, K+ purplish spores uniseriate, 8–10 × 5–6 µm, warty	<i>Pronectria subimperspicua</i> (Speg.) Lowen	
21.	Perithecia superficial; pink or reddish; wall K–		22
22.	Perithecia pink, fuzzy; spores of two sizes		
	 [<i>Ovicuculospora parmeliae</i> (Berk. & M. A. Curtis) Etayo]		
22.	Perithecia reddish with short colorless setae; spores all one size; on various crustose lichens (incl. <i>Micarea prasina</i>)		
	 <i>Nectriopsis rubefaciens</i> (Ellis & Everh.) M.S. Cole & D. Hawksw.		
20.	Perithecia black		23
23.	Asci 8-spored; on <i>Haematomma persoonii</i>		
	 <i>Lichenochora haematommatum</i> R.C. Harris & Lendemer		
23.	Asci 16-spored (part spores); part spores tetrahedral; perithecia with setae around ostiole; in thallus of <i>Punctelia rudecta</i>		
	 <i>Trichosphaerella buckii</i> R.C. Harris & Lendemer		
1.	Spores not produced in asci, but rather in flask-shaped or disciform structures (pycnidia, sporodochia), tiny stromata (<i>Phaeosporobolus</i>) or basidiomata (<i>Tremella</i>) or from hyphae embedded in thallus or apothecia ("hyphomycetes")		24
24.	Spores produced in pycnidia, sporodochia, or tiny stromata		25
25.	Spores brown or greenish		26
26.	Conidioma a pycnidium		27
27.	Conidia 1-septate		28
28.	Conidia formed in short chains, greenish; on apothecia and thallus of <i>Lecanora louisianae</i> , <i>L. subpallens</i> and <i>Pyrrospora varians</i>		
	 <i>Vouauxiella lichenicola</i> Petr. & Syd.		
28.	Conidia not formed in chains, brown; on <i>Pertusaria</i>		
	 <i>Lichenodiplis lecanorae</i> (Vouaux) Dyko & D. Hawksw.		
27.	Conidia simple		29
29.	Conidia irregularly shaped, 8–13 × 5–6 µm; on <i>Leiorreuma</i> and <i>Phaeographis</i> ...		
	 <i>Coniambigua phaeographidis</i> Etayo & Diederich		
29.	Conidia ± globose to pyriform		30
30.	Conidia globose, 5–6 × 4.5–5 µm; on <i>Lecanora hybocarpa</i>		
	 <i>Lichenocodium lecanorae</i> (Jaap) D. Hawksw.		
30.	Conidia pyriform, 8–10 × 3–3.5 µm; on <i>Parmotrema subrigidum</i>		
	 <i>Lichenocodium cargillianm</i> (Linds.) D. Hawksw.		
26.	Conidioma a sporodochium or tiny superficial stroma		31
31.	Conidia produced in sporodochia		32
32.	Exciple orange red; conidia simple, 4.7–5.8 × 3–4 µm; on <i>Pertusaria epixantha</i>		
	 <i>Minutoexcipula miniatorexcipula</i> R.C. Harris & Lendemer		
32.	Exciple brown; conidia 1-septate		33
33.	Conidia 6.5–8 × 3–4 µm; on <i>Pertusaria texana</i>		
	 <i>Minutoexcipula tuckerae</i> V. Atienza & D. Hawksw.		
33.	Conidia 6–7.5 × 2.5–3.5 µm; on <i>Pertusaria pustulata</i> and <i>P. subpervetusa</i> ...		
	 <i>Minutoexcipula mariana</i> V. Atienza		
31.	Conidia produced in tiny orbicular or slightly irregular stromata; conidia muriform, ± globose		34
34.	On various crustose lichens, especially <i>Phaeographis</i> and <i>Leiorreuma</i>		
	 <i>Etayoa tryptethelii</i> (Flakus & Kukwa) Diederich & Ertz		
34.	On <i>Ochrolecia</i> and <i>Pertusaria</i>	<i>Phaeosporobolus alpinus</i> R. Sant. et al.	
25.	Spores colorless		35
35.	Conidia broadly ellipsoid, 3.5–6 × 3–4 µm, with a single guttule; on Parmeliaceae, esp. <i>Punctelia rudecta</i>	<i>Didymocyrtis melanelixiae</i> (Brackel) Diederich, R.C. Harris & Etayo (<i>Phoma</i> asexual stage)	
35.	Conidia tetrahedral (triangular in surface view); apices papillate on <i>Pertusaria subpervetusa</i>	<i>Cornutispora triangularis</i> Diederich & Etayo	

11. Thallus black, ridged and pustulose; apothecia densely white pruinose..... *Collema pulcellum* Ach. var. *leucopeplum* (Tuck.) Degel.
11. Thallus varying shades of gray, not ridged and pustulose; apothecia not densely white pruinose ... 12
12. Thallus composed of overlapping squamules, without distinct marginal radiating lobes..... *Fuscopannaria leucosticta* (Tuck.) P. M. Jørg.
12. Thallus truly foliose, with distinct marginal lobes 13
13. Thallus gelatinous (jelly-like) when wet 14
14. Lower surface with abundant rhizines *Pannaria lurida* (Mont.) Nyl. subsp. *quercicola* P. M. Jørg.
14. Lower surface without rhizines 15
15. Thallus smooth *Leptogium azureum* (Sw.) Mont.
15. Thallus wrinkled *Leptogium corticola* (Taylor) Tuck.
13. Thallus not gelatinous (not jelly-like) when wet 16
16. Thallus lead gray; with a distinct weft of dark rhizines; main photobiont a cyanobacterium *Coccocarpia erythroxyli* (Spreng.) Swinsc. & Krog
16. Thallus gray to greenish; with pale rhizines if rhizines are present; main photobiont a green alga *Lobaria ravenelii* (Tuck.) Yoshim.

KEY 4. FOLIOSE CHLOROLICHENS

1. Thallus not pustulose, sorediate, isidiate, or phyllidiate; apothecia often present 2
2. Thallus with a distinct black, felt-like hypothallus on the lower surface; very rare..... *Anzia colpodes* (Ach.) Stizenb.
2. Thallus with a naked lower surface or with rhizines, but not with a distinct black, felt-like hypothallus; common 3
3. Lobes broad, >3 mm wide; ascospores hyaline 4
4. Lobes adnate; thallus wrinkled, scrobiculate upper surface; medulla C+ pink (gyrophoric acid present); rare *Lobaria ravenelii* (Tuck.) Yoshim.
4. Lobes adnate or ascending; thallus with a smooth upper surface; medulla C- other substances present) 5
5. Apothecia entire, not perforated with a hole in the center; medulla P+ red (protocetraric acid present) *Parmotrema submarginale* (Michx.) DePriest & B. Hale
5. Apothecia perforated with a hole in the center; medulla P- or P+ yellow (alecoronic and/or norstictic acid present) 6
6. Medulla UV- (alecoronic acid absent); typically inland *Parmotrema perforatum* (Jacq.) A. Massal.
6. Medulla UV+ bright blue-white (alecoronic acid present); typically coastal, rarer inland 7
7. Medulla, especially near the apothecia, K- (norstictic acid absent) *Parmotrema subrigidum* Egan s. str.
7. Medulla, especially near the apothecia, K+ yellow turning red (norstictic acid present) *Parmotrema subrigidum* Egan s. lat.
3. Lobes narrow, <3 mm wide; ascospores brown or hyaline 8
8. Thallus dark greenish-brown to brown, forming minute rosettes on conifer branches..... *Tuckermanella fendleri* (Nyl.) Essl.
8. Thallus gray to blue-gray or light brownish, not forming minute rosettes on conifer branches .. 9
9. Medulla K+ pink turning dark brown (lividic acid present); ascospores hyaline..... *Hypotrachyna livida* (Taylor) Hale
9. Medulla K- or K+ yellow (atranorin present or absent); ascospores brown 10
10. Lower surface black; medulla UV+ blue-white (sekikaic acid present); primarily coastal *Dirinaria confusa* D.D. Awasthi
10. Lower surface white or pale brownish; medulla UV- (sekikaic acid absent); inland and coastal 11
11. Upper cortex and medulla K+ yellow (atranorin present); lobes not abundantly lobulate *Physcia pumiliator* R.C. Harris
11. Upper cortex and medulla K- (atranorin absent); lobes abundantly lobulate *Anaptychia palmulata* (Michx.) Vain.
1. Thallus pustulose, sorediate, isidiate, or phyllidiate; apothecia uncommon 12

12. Thallus with a distinct black, felt-like hypothallus on the lower surface; lobe margins abundantly isidiate/ phyllidiate **Anzia ornata (Zahlbr.) Asahina**
12. Thallus with a naked lower surface or with rhizines, but not with a distinct black, felt-like hypothallus ... 13
13. Thallus isidiate or lobulate 14
14. Thallus lobulate.....
15. Lower surface black, at least centrally; lobules fine, erect, fragile.....
..... **Phaeophyscia squarrosa Kashiw.**
15. Lower surface plae to tan throughout; lobules coarse and robust, not erect, not fragile
..... **Anaptychia palmulata (Michx.) Vain.**
14. Thallus isidiate 16
16. Lower surface ecorticate, orange pigmented; orange pigment K+ purple
..... **Heterodermia crocea R.C. Harris**
16. Lower surface corticate, not orange pigmented 17
17. Medulla C+ pink or red (gyrophoric or lecanoric acid present) 18
18. Lobes broad, >3 mm wide 19
19. Lower surface pale; upper surface with conspicuous white pseudocyphellae; conspicuous marginal cilia absent 20
20. Thallus isidiate; isidia short to tall, cylindrical, brown tipped, not clustered only in the pseudocyphellae.....
..... **Punctelia rudecta (Ach.) Krog**
20. Thallus with squamiform soredia that resemble isidia; "isidia" short, squamiform, poorly corticate, not brown tipped, always clustered in the pseudocyphellae
..... **Punctelia missouriensis G. Wilh. & Ladd**
19. Lower surface black towards the center and brown towards the margin; upper surface without conspicuous white pseudocyphellae; conspicuous marginal cilia present 21
21. Upper surface yellow-green, K-, KC+ strong yellow (usnic acid present) **Parmotrema madagascariaceum (Hue) Hale**
21. Upper surface blue-gray, K+ yellow, KC- (atranorin present)
..... **Parmotrema tinctorum (Nyl.) Hale**
18. Lobes narrow, <3 mm wide 22
22. Marginal cilia with bulbate bases; lower surface brown
..... **Bulbothrix scortella (Nyl.) Hale**
22. Marginal cilia without bulbate bases; lower surface black.....
..... **Hypotrachyna minarum (Vain.) Krog & Swinsc.**
17. Medulla C- (gyrophoric or lecanoric acid absent) 23
23. Medulla P+ orange or red (protocetraric acid, salazinic acid or stictic acid present) 24
24. Marginal cilia present, with bulbate bases; lobes narrow, <3 mm wide
..... **Bulbothrix isidiza (Nyl.) Hale**
24. Marginal cilia present or absent, but always lacking bulbate bases; lobes broad, >3 mm wide 25
25. Medulla K+ yellow turning dirty brown (protocetraric or stictic acid present); marginal cilia absent to sparse 26
26. Medulla P+ orange (stictic acid present together with norlobaridone); upper surface without pseudocyphellae ...
..... **Parmotrema internexum (Nyl.) Hale**
26. Medulla P+ red (protocetraric acid present); upper surface with white pseudocyphellae.....
..... **Canoparmelia amazonica (Nyl.) Elix & Hale**
25. Medulla K+ yellow turning red (salazinic acid present); marginal cilia usually conspicuously present and abundant 27
27. Lower portions of medulla UV+ bright yellow (lichexanthone present) **Parmotrema ultralucens (Krog) Hale**
27. Entire medulla UV- 28
28. Lower surface black.....
..... **Parmotrema subsidiosum (Müll. Arg.) Hale**
28. Lower surface brown.....
..... **Parmotrema neotropicum Kurok.**

23. Medulla P- (salazinic acid and stictic acid absent) 29
29. Lobes broad, >3 mm wide 30
30. Lobes adnate; margins without long conspicuous cilia
..... *Canoparmelia caroliniana* (Nyl.) Elix & Hale
30. Lobes ascending; marginal with long conspicuous cilia 31
31. Medulla UV+ blue-white (alecoronic acid present); upper
cortex blue-gray, K+ yellow, KC- (atranorin present)
..... *Parmotrema mellissii* (C.W. Dodge) Hale
31. Medulla UV- (fatty acids present); upper cortex yellow-
green, K-, KC+ yellow gold (usnic acid present)
..... *Parmotrema xanthinum* (Müll. Arg.) Hale
29. Lobes narrower, <3 mm wide 32
32. Isidia never ciliate, often breaking down into piles that resemble
soralia with large coarse soredia; lobes tightly adnate; medulla
UV+ blue-white (divaricatic acid present); primarily coastal in the
DRBH *Dirinaria aegialita* (Ach.) B.J. Moore
32. Isidia ciliate, never breaking down into soralia; lobes adnate, but
not tightly so; medulla UV- (divaricatic acid absent); throughout
the DRBH .. *Hypotrachyna horrescens* (Taylor) Swinsc. & Krog
13. Thallus pustulose or sorediate 33
33. Upper cortex UV+ bright yellow (lichexanthone present) 34
34. Medulla white; lower surface with dichotomously branched and forking rhizines
..... *Hypotrachyna ossealba* (Vain.) Y.S. Park & Hale
34. Medulla yellow or orange pigmented; lower surface with simple or forking rhizines 35
35. Lobes with dactyls along the margins *Pyxine caesiopruinosa* (Nyl.) Imshaug
35. Lobes with discrete, laminal and marginal soralia 36
36. Lobe tips typically with discrete white "pads" of pruina; medulla K-
..... *Pyxine subcinerea* Stirt.
36. Lobe tips without discrete white "pads" of pruina; medulla K+ purple (but
often difficult to detect) *Pyxine albovirens* (G. Mey.) Aptroot
33. Upper cortex UV- (lichexanthone absent) 37
37. Lower surface ecorticate 38
38. Lower surface yellow or orange pigmented, at least in spots near the lobe tips 39
39. Lower surface orange pigmented; pigment K+ purple
..... *Heterodermia obscurata* (Nyl.) Trevis.
39. Lower surface with spots of yellow pigment near the lobe tips; pigment K-
..... *Heterodermia casarettiana* (A. Massal.) Trevis.
38. Lower surface not yellow or orange pigmented 40
40. Lobes elongate, linear, strap-shaped, +/- ascending
..... *Heterodermia leucomelos* (L.) Poelt
40. Lobes not linear and strap-shaped, always adnate 41
41. Lower surface weakly corticate; upper surface shiny, not appearing
frosted; medulla K+ yellow turning red but without norstictic acid
crystals (salazinic acid present)
..... *Heterodermia albicans* (Pers.) Swinsc. & Krog
41. Lower surface entirely ecorticate; upper surface appearing frosted with
a white pruina; medulla K+ yellow (salazinic acid absent)
..... *Physcia atrostriata* Moberg
37. Lower surface corticate 42
42. Medulla orange-red or yellow pigmented 43
43. Medulla strongly orange-red pigmented; pigment K+ purple
..... *Phaeophyscia rubropulchra* (Degel.) Essl.
43. Medulla yellow pigmented; pigment K- 44
44. Thallus with discrete soralia; medulla strongly yellow pigmented
..... *Pyxine sorediata* (Ach.) Mont.
44. Thallus with laminal or marginal pustules; medulla weakly yellow
pigmented 45
45. Medulla C+ pink (gyrophoric acid present); thallus with coarse
pustules *Hypotrachyna spumosa* (Asahina) Krog & Swinsc.

45. Medulla C- (gyrophoric acid absent); thallus with diffuse pustules
..... ***Myelochroa aurulenta* (Tuck.) Elix & Hale**
42. Medulla white 46
46. Upper surface yellow or yellow green (calycin or usnic acid present) 47
47. Soralia marginal/terminal, not laminal; upper surface yellow, KC- (calycin present) ***Candelaria concolor* (Dicks.) Stein**
47. Soralia laminal; upper surface yellow-green, KC+ yellow (usnic acid present) 48
48. Lobes broad, >3 mm wide; medulla P+ orange-red, UV- (protocetraric acid present) ***Flavoparmelia caperata* (L.) Hale**
48. Lobes narrow, <1 mm wide; medulla P-, UV+ blue-white (divaricatic acid present) ***Parmeliopsis subambigua* Gyeln.**
46. Upper surface blue-gray or gray-brown (atranorin present or absent) 49
49. Upper cortex gray-brown, K- (atranorin absent); capitate soralia terminal on the tips of secondary lobes
..... ***Phaeophyscia pusilloides* (Zahlbr.) Essl.**
49. Upper cortex blue-gray, K+ yellow (atranorin present); soralia not as above 50
50. Medulla C+ pink-red (gyrophoric or lecanoric acid present) 51
51. Lower surface pale; upper surface with conspicuous white pseudocyphellae; squamiform soredioid-isidia present and clustered in the pseudocyphellae
..... ***Punctelia missouriensis* G. Wilh. & Ladd**
51. Lower surface black; upper surface without conspicuous white pseudocyphellae; soralia or pustules present 52
52. Thallus with discrete soralia; rare
.. ***Hypotrachyna cryptochlora* (Vain.) D. Hawksw. & A. Crespo**
52. Thallus with coarse pustules; common
.. ***Hypotrachyna spumosa* (Asahina) Krog & Swinsc.**
50. Medulla C- (gyrophoric or lecanoric acid absent) 53
53. Medulla K+ yellow turning red (salazinic acid or norstictic acid present) 54
54. Lobes narrow, <3 mm wide; black marginal cilia absent
..... ***Heterodermia albicans* (Pers.) Swinsc. & Krog**
54. Lobes broad, >3 mm wide; black marginal cilia present .. 55
55. Lobes strongly ascending; lower surface with broad white blotches especially near the margins .. 56
56. Medulla K+ yellow turning red, producing norstictic acid crystals, P+ yellow (norstictic acid present)
..... ***Parmotrema hypotropum* (Nyl.) Hale**
56. Medulla K+ yellow turning red, not producing norstictic acid crystal, P+ orange (stictic acid present) ... ***Parmotrema hypoleucinum* (J. Steiner) Hale**
55. Lobes not strongly ascending; lower surface entirely black in the center and brown towards the margins 57
57. Capitate soralia with fine soredia present on the tips of the sublobes
..... ***Parmotrema reticulatum* (Taylor) M. Choisy**
57. Diffuse soralia with coarse soredia present on the tips of the sublobes and lobes as well as on the thallus surface
..... ***Parmotrema subsidiosum* (Müll. Arg.) Hale**
53. Medulla K- or K+ yellow-brown, but not K+ yellow turning red 58

58. Medulla P+ orange or red (protocetraric acid or stictic acid present) 59
59. Medulla P+ orange (stictic acid present); thallus surface scrobiculate *Crespoa crozalsiana* (Harm.) Lendemer & B.P. Hodk.
59. Medulla P+ red (protocetraric acid present); thallus surface smooth, not scrobiculate 60
60. Echinocarpic acid absent; common [TLC required] *Parmotrema gardneri* (C.W. Dodge) Sérus.
60. Echinocarpic acid present; rare [TLC required] *Parmotrema dilatatum* (Vain.) Hale
58. Medulla P- (protocetraric acid or stictic acid absent) ... 61
62. Lobes broad, >3 mm wide 63
63. Medulla UV- (fatty acids present)..... *Parmotrema praesorediosum* (Nyl.) Hale
63. Medulla UV+ blue-white (aletronic acid present) 64
64. Thallus with marginal soralia *Parmotrema rampoddense* (Nyl.) Hale
64. Thallus with coarse, laminal soredia that arise from the breakdown of isidia *Parmotrema mellissii* (C.W. Dodge) Hale
62. Lobes narrow, <3 mm wide 65
65. Medulla UV+ blue-white (divaricatic acid present) *Dirinaria picta* (Sw.) Schaer. ex Clem.
65. Medulla UV- (divaricatic acid present) 66
66. Lower surface black..... *Physcia solediosa* (Vain.) Lynge
66. Lower surface pale 67
67. Thallus with discrete, laminal soralia; upper surface often pruinose; common *Physcia americana* G. Merr.
67. Thallus with continuous, marginal soralia; upper surface epruinose; rare *Physcia millegrana* Degel.

KEY 5. CLADONIACEAE

1. Podetia present; thallus with or without primary squamules 2
2. Podetia abundantly branching and forming cushions on the ground 3
3. Podetia corticate; apothecia/pycnidia red *Cladonia leporina* Fr.
3. Podetia ecorticate; apothecia/pycnidia pallid to brown or unknown 4
4. Podetia (especially near the tips) P-, UV+ blue-white (perlatolic acid present); restricted to barrier islands in the DRBH *Cladonia evansii* Abbayes
4. Podetia (especially near the tips) P+ red, UV- (fumarprotocetraric acid present); common on roadsides and sandy soils throughout the DRBH *Cladonia subtenuis* (Abbayes) Mattick
2. Podetia simple or little branching, but not forming cushions on the ground 5
5. Podetia with a continuous cortex, not sorediate or microsquamulose 6
6. Podetia forming multi-tiered cups that proliferate from the centers, resembling a wedding cake *Cladonia rappii* A. Evans
6. Podetia not forming cups 7

7. Apothecia/pycnidia red; primary squamules conspicuously sorediate; thallus P- *Cladonia incrassata* Flörke
7. Apothecia/pycnidia brown; primary squamules esorediate; thallus P+ yellow, orange or red 8
8. Podetia tall, little branching, forming funnels; thallus UV+ blue-white and P+ yellow (baeomycesic acid and squamatic acid present) *Cladonia atlantica* A. Evans
8. Podetia short, blunt, not forming funnels; thallus UV- or UV+ dull white, P+ orange or red (fumarprotocetraric acid or stictic acid present) 9
9. Podetia slender, conspicuously overtopped by large brown apothecia; primary squamules small, not lobed, decumbent and overlapping; fumarprotocetraric acid present *Cladonia peziziformis* (With.) J.R. Laundon
9. Podetia broad, not conspicuously overtopped by the brown apothecia; primary squamules large, lobed, erect; atranorin, norstictic acid and stictic acid present *Cladonia polycarpia* G. Merr.
5. Podetia with a discontinuous cortex, with some parts dissolving into soredia or microsquamules .. 10
10. Apothecia/pycnidia red 11
11. Podetia sorediate, with the soredia abrading to reveal remnants of the loose medulla or the opaque white stereome; thallus P- (barbatic acid present) *Cladonia macilenta* var. *bacillaris* (Genth) Schaer.
11. Podetia microsquamulose, with the microsquamules sloughing off to reveal the naked translucent stereome; thallus P- (barbatic acid present) or P+ orange (thamnolic acid present) 12
12. Thallus P+ orange (thamnolic acid present) *Cladonia didyma* var. *vulcanica* (Zoll. & Moritz) Vain.
12. Thallus P- (barbatic acid present). *Cladonia didyma* var. *didyma* (Fée) Vain.
10. Apothecia/pycnidia brown 13
13. Thallus UV+ blue-white and P+ yellow (squamatic acid and baeomycesic acid present) *Cladonia beaumontii* (Tuck.) Vain.
13. Thallus UV- and P+ orange or red (other substances present) 14
14. Thallus K+ instantly lemon yellow, P+ orange (thamnolic acid present) 15
15. Squamules small, +/- erect, dissolving into "isidioid" microsquamules; podetia slender, covered with microsquamules, the microsquamules sloughing off to reveal the naked translucent stereome *Cladonia parasitica* (Hoffm.) Hoffm.
15. Squamules large, decumbent, not dissolving into microsquamules; podetia short, broad, covered with coarse squamules that are not easily dislodged *Cladonia santensis* Tuck.
14. Thallus K- or K+ dingy yellow-brown, P+ red (fumarprotocetraric acid present) ... 16
16. Primary squamules small, not distinctly lobed, entirely dissolving into soredia; podetia often deformed and tortuous *Cladonia ramulosa* (With.) J.R. Laundon
16. Primary squamules large, lobed, not entirely dissolving into soredia; podetia blunt, never deformed and tortuous 17
17. Podetia with the basal portions remaining corticate, often with sorediate patches in the lower portions admixed with intact corticate areas; microsquamules absent *Cladonia ochrochlora* Flörke
17. Podetia with the basal portions microsquamulose, often with the upper and middle portions coarsely sorediate; microsquamules present *Cladonia subradiata* (Vain.) Sandst.
1. Podetia absent; thallus entirely composed of primary squamules 18
18. Conspicuous apothecia present, borne directly on a short stipe arising from the primary squamules .. *Cladonia caespiticia* (Pers.) Flörke
18. Apothecia absent 19
19. Thallus P-; pycnidia red 20
20. Primary squamules large, broad, little lobed, conspicuously sorediate; squamatic acid present *Cladonia incrassata* Flörke
20. Primary squamules small, lobes, not conspicuously sorediate; barbatic acid present *Cladonia macilenta* var. *bacillaris* (Genth) Schaer.

19. Thallus P+ yellow, orange or red; pycnidia brown or red 21
21. Thallus P+ yellow (baeomycesic acid present) 22
 22. On sandy soil in disturbed areas *Cladonia atlantica* A. Evans
 22. On bark or rotting wood in swamps *Cladonia beaumontii* (Tuck.) Vain.
21. Thallus P+ orange or red (fumarprotocetraric acid, stictic acid, or thamnolic acid present) ... 23
 23. Thallus K+ instantly lemon yellow (thamnolic acid present) 24
 24. Primary squamules robust, broad, little lobed, not dissolving *Cladonia santensis* Tuck.
 24. Primary squamules fragile, narrow, lobed, often dissolving 25
 25. Primary squamules often entirely dissolving into "isidioid" microsquamules; pycnidia brown *Cladonia parasitica* (Hoffm.) Hoffm.
 25. Primary squamules typically remaining intact, sometimes dissolving into soredia; pycnidia red *Cladonia didyma* var. *vulcanica* (Zoll. & Moritz) Vain.
23. Thallus K- or K+ dingy yellow-brown 26
26. Thallus P+ orange (stictic acid present); squamules erect, not dissolving *Cladonia polycarpia* G. Merr.
26. Thallus P+ red (fumarprotocetraric acid present); squamules plane or decumbent, dissolving or not 27
 27. Primary squamules dissolving entirely into soredia *Cladonia ramulosa* (With.) J.R. Laundon
 27. Primary squamules remaining intact, at least for the most part 28
 28. Primary squamules small, overlapping and decumbent, not lobed *Cladonia peziziformis* (With.) J.R. Laundon
 28. Primary squamules large, not overlapping and decumbent, lobed *Cladonia ochrochlora* Flörke or *Cladonia subradiata* (Vain.) Sandst.

KEY 6. FRUTICOSE MACROLICHENS (EXCLUDING CLADONIACEAE)

1. Thallus bright orange-yellow, K+ purple 2
 2. Thallus sorediate; apothecia rare and often absent; branches elongate, slender [Teloschistes flavicans (Sw.) Norman]
 2. Thallus esorediate, apothecia often present; branches short, blade-like *Teloschistes chrysophthalmus* (L.) Norm.
1. Thallus gray or yellow-green, not K+ purple 3
 3. Branches solid without a central cord or cavity 4
 4. Branches smooth 5
 5. Branches completely flattened to the tips; perlatolic acid present *Ramalina stenospora* Müll. Arg.
 5. Branches rounded except near the base; divaricatic or homosekikaic acid present [Ramalina montagnei De Not.]
 4. Branches with abundant raised tubercles or with ridges and depressions 6
 6. Apothecia on the surface of the branches or along the margins *Ramalina complanata* (Sw.) Ach.
 6. Apothecia on the tips of the branches 7
 7. Branches with conspicuous white tubercles; salazinic acid present or protocetraric acid present *Ramalina willeyi* R. Howe
 7. Branched without conspicuous white tubercles; but with ridges and depressions; various substances other than the above 8
 8. Medulla with lichen substances present (TLC required) *Ramalina culbersoniorum* LaGreca
 8. Medulla without lichen substances (TLC required) [Ramalina americana Hale, present just north of DRBH]
 3. Branches with a central cord or cavity 9
 9. Thallus without soredia or isidia; apothecia typically present 10
 10. Restricted to coastal maritime forests; medulla white; branches often weakly foveolate or ridged; fibrils regularly arranged; galbinic acid present *Usnea evansii* Motyka
 10. Restricted to inland habitats; medulla white or red; branches never foveolate or ridged; fibrils haphazardly arranged; galbinic acid absent 11

21. Ascospores averaging $\geq 9 \mu\text{m}$ long; medulla pink-red pigmented; norstictic acid present or absent 12

12. Norstictic acid present *Usnea endochrysea* Stirt. s. str.

12. Norstictic acid absent *Usnea endochrysea* Stirt. s. lat.

11. Ascospores averaging $< 9 \mu\text{m}$ long; medulla often white, sometimes pink-red pigmented; norstictic present or absent 13

13. Norstictic acid present *Usnea strigosa* (Ach.) Eaton s. str.

13. Norstictic acid absent 14

14. Psoromic acid present *Usnea strigosa* (Ach.) Eaton s.l.

14. Psoromic acid absent 15

15. Thamnolic acid present *Usnea strigosa* (Ach.) Eaton s.l.

15. Thamnolic acid absent *Usnea strigosa* (Ach.) Eaton s.l.

9. Thallus sorediate or isidiate; apothecia rarely present 16

16. Medulla pink-red pigmented 17

17. Branches with a central cord; medulla P- (fatty acids present); common *Usnea mutabilis* Stirt.

17. Branches with a central cavity; medulla P+ yellow (norstictic acid present); rare *Usnea baileyi* (Stirt.) Zahlbr.

16. Medulla white 18

18. Thallus long, pendant; branches with white rings (annular pseudocyphellae) *Usnea trichodea* Ach.

18. Thallus short, shrubby; branches without white rings 19

19. Cortex red pigmented, pigment often mottled *Usnea pensylvanica* Motyka

19. Cortex not red pigmented 20

20. Medulla P+ orange-red (protocetraric acid present) *Usnea subscabrosa* Motyka s. str.

20. Medulla P- (protocetraric acid absent) *Usnea subscabrosa* Motyka s. lat.

KEY 7. FOLIICOLOUS CRUSTOSE LICHENS

1. On leaves of *Persea*, especially in inland swamps; thallus forming tiny shiny greenish areoles, each with a central black pycnidium; only pycnidia observed; apothecia and ascospores unknown in MACP..... *Asterothyrium decipiens* (Rehm) R. Sant. ?

1. On leaves of *Sabal minor* or *Ilex*; thallus areolate or not, with either pale tan pycnidia or tall black sterile setae .. 2

2. On leaves of *Sabal minor*; thallus areolate, with pale tan pycnidia; conidia bacilliform; apothecia and ascospores unknown in MACP material *Fellhanera bouteillei* (Desm.) Vezda

2. On leaves of *Ilex*; thallus continuous, with tall black sterile setae; apothecia and ascospores unknown in MACP material [*Tricharia santessonii* D. Hawks.]

KEY 8. TYPICALLY ASEXUALLY REPRODUCING CRUSTOSE LICHENS

1. Thallus with specialized structures (e.g., hyphophores, stalked pycnidia) for the dispersal of non-lichenized diaspores (conidia); lichenized diaspores (e.g., isidia, soredia, granules) absent 2

2. Thallus with hyphophores (darkened structures that resemble apically widened hairs) 3

3. Hyphophores tall, erect, not apically widened, resembling an eyelash *Gyalideopsis buckii* Lücking et al.

3. Hyphophores short, bent down, apically widened, resembling a tiny bent shovel [*Gyalideopsis ozarkensis* Lücking & W. R. Buck]

2. Thallus with pale stalked pycnidia or pale synnemata (stalked sporodochia) 4

4. Thallus with pale synnemata (stalked sporodochia); conidia compound aggregations of round cells [*Dictyocatenulata alba* Finley & E.F. Morris]

4. Thallus with pale stalked pycnidia; conidia simple, ellipsoid 5

5. Thallus UV+ blue-white (lobaric acid present), often P+ orange-red (fumarprotocetraric acid present) *Micarea neostipitata* Coppins & P. May

5. Thallus UV- and P- (lobaric and fumarprotocetraric acid absent) [*Micarea pycnidiophora* Coppins & P. James]

1. Thallus without specialized structures for the dispersal of non-lichenized diaspores; lichenized diaspores present 6

6. Photobiont *Trentepohlia* 7

7.	Thallus sorediate	8
8.	Soralia irregular in shape, diffuse; soredia light yellow-brown; thallus P-, typically indistinct and immersed in the substrate	<i>Opegrapha corticola</i> Coppins & P. James
8.	Soralia discrete, punctiform; soredia white to gray; thallus P+ orange (stictic acid present), typically distinct and white to gray in color	<i>Nadvornikia sorediata</i> R.C. Harris
7.	Thallus isidiolate	9
9.	Thallus dark brown to gray	<i>Pseudosagedia isidiata</i> (R.C. Harris) R.C. Harris
9.	Thallus yellow-brown, often bronze in color	10
10.	Thallus smooth and shiny; isidia typically short, +/- globose and inconspicuous; perithecia often present, dark brown-black, covered with apical setae	<i>Trichothelium americanum</i> Lendemer
10.	Thallus roughened and dull; isidia typically tall, often coralloid, conspicuous; perithecia often present, concolorous with the thallus, smooth or covered with short isidia, but never with black setae	<i>Porina scabrata</i> R.C. Harris
6.	Photobiont coccoid	11
11.	Thallus yellow or orange	12
12.	On rock (concrete); thallus orange, K+ purple	<i>Caloplaca flavocitrina</i> (Nyl.) H. Olivier
12.	On bark or wood; thallus yellow, K-	13
13.	Thallus C+ or KC+ yellow-orange (xanthoness present)	14
14.	Thallus composed of flat green areoles with small, discrete, often marginal soralia; soredia yellow; typically on hardwoods	<i>Buellia wheeleri</i> R.C. Harris
14.	Thallus composed of orange-yellow granules (leprose); soralia or soredia absent; typically on conifers	<i>Pyrrhospora</i> sp. nov.
13.	Thallus C- and KC- (xanthoness absent)	15
15.	Thallus areolate, with the areoles dissolving into piles of soredia; apothecia not uncommon	<i>Candelariella xanthostigmoides</i> (Müll. Arg.) R.W. Rogers
15.	Thallus leprose, composed of granules of various sizes; apothecia unknown in MACP material	16
16.	Granules minute (>10 µm in diameter); thallus thin, dull yellow in color (rhizocarpic acid present); on conifers in humid, swampy forests	<i>Chrysothrix chamaecyparicola</i> Lendemer
16.	Granules larger (>25–45 µm in diameter); thallus thicker, intense bright yellow in color (pinastric acid present); on conifers and hardwoods, often in upland habitats	<i>Chrysothrix xanthina</i> (Vain.) Kalb
11.	Thallus green, gray, or brown	17
17.	Thallus C+ pink (gyrophoric or lecanoric acid present; always confirm in squash mount if C- under the dissecting microscope)	18
18.	Thallus isidiolate	<i>Placynthiella icmalea</i> (Ach.) Coppins & P. James
18.	Thallus sorediate	19
19.	Thallus lead gray, with dark blue-gray soredia	<i>Trapeliopsis flexuosa</i> (Fr.) Coppins & P. James
19.	Thallus not lead gray, soredia various colors	20
20.	Thallus light gray, continuous; "soralia" regular and discoid; on hardwoods	<i>Varicellaria velata</i> (Turner) I. Schmitt & Lumbsch
20.	Thallus green or brown-green, areolate; soralia irregular and dissolving the areoles; on rotting wood, organic matter, or rarely the base of <i>Pinus</i>	<i>Placynthiella dasaea</i> (Stirt.) Tønsberg
17.	Thallus C- (gyrophoric or lecanoric acid absent)	21
21.	Thallus UV+ bright yellow (lichexanthone present)	22
22.	Thallus coarsely pustulate; medulla of pustules K- (zeorin present)	<i>Megalospora pachycheila</i> (Tuck.) Sipman
22.	Thallus with densely pruinose apothecia resembling discrete; "soralia" K+ various colors (zeorin absent)	23
23.	Medulla of "soralia" K+ yellow rapidly turning lavender, P- (hypothamnolic acid present)	<i>Variolaria hypothamnolica</i> (Dibben) ined.
23.	Medulla of "soralia" K+ yellow slowly turning dirty brownish or rapidly turning deep reddish-brown, P+ orange (haemathamnolic or thamnolic acid present)	24
24.	Medulla of "soralia" K+ yellow rapidly turning deep reddish-brown (haemathamnolic acid present); common	<i>Variolaria commutata</i> (Müll. Arg.) ined.

24. Medulla of "soralia" K+ yellow slowly turning dirty brownish (thamnolic acid present); rare *Variolaria trachythallina* (Erichsen) Lendemer et al.
21. Thallus UV- or UV+ blue-white, but not UV+ bright yellow (lichexanthone absent) 25
25. Thallus K- and KC+ yellow (usnic acid present) 26
26. Thallus with a well developed, fibrous, white prothallus [*Lecanora thysanophora* R.C. Harris]
26. Thallus without a well developed, fibrous, white prothallus 27
27. Thallus areolate, with discrete circular soralia *Lecanora floridula* Lumbsch
27. Thallus granular to areolate, without discrete circular soralia 28
28. Decarboxysquamic acid present (TLC needed) *Lecanora strobilina* (Spreng.) Kieff.
28. Decarboxysquamic acid absent (TLC needed) *Lecanora cf. strobilina* (Spreng.) Kieff.
25. Thallus K- or K+ yellow, always KC- (usnic acid or xanthenes absent) 29
29. Thallus P+ intense yellow, orange, or orange-red (fumarprotocetraric acid, pannarin, psoromic acid or thamnolic acid present) 30
30. Thallus P+ intense yellow (psoromic acid present) *Phlyctis boliviensis* Nyl.
30. Thallus P+ orange or orange-red 31
31. Thallus entirely leprose, composed of granules (*Lepraria*) 32
32. Thallus thin, the granules not supported by a well developed hypothallus, P+ orange-red (fumarprotocetraric acid present); rare, usually associated with *Taxodium* *Lepraria friabilis* Lendemer, K. Knudsen & Elix
32. Thallus thick, the granules supported on a well developed hypothallus, P+ orange 33
33. Thallus K+ instantly intense yellow (thamnolic acid present) *Lepraria aurescens* Orange & Wolesley
33. Thallus K- or K+ weak, dirty yellow or brownish (other substances present) 34
34. Gray to blue-green in color, never with a distinctly yellowish hue; stictic acid present; **very common** [if lacking TLC use this name] *Lepraria finkii* (B. de Lesd.) R.C. Harris
34. Blue-green to whitish in color, but always with a distinct yellowish hue; dibenzofurans present; **very rare** [if lacking TLC do not use this name] *Lepraria vouauxii* (Hue) R.C. Harris
31. Thallus continuous or areolate, not leprose, with soralia or pustules 35
35. Thallus K+ intense yellow, P+ orange (thamnolic acid present) 36
36. Thallus pustulose, without discrete soralia *Variolaria pustulata* (Brodo & W. L. Culb.) Lendemer et al.
36. Thallus not pustulose, with discrete "soralia" *Variolaria trachythallina* (Erichsen) Lendemer et al.
35. Thallus K- or K+ weak dirty yellow, P+ orange-red (fumarprotocetraric acid or pannarin present) 37
37. Thallus pustulose, without discrete soralia, K-, P+ orange-red (pannarin present) *Megalospora porphyritis* (Tuck.) R.C. Harris
37. Thallus soraliate, without pustules, K- dirty yellow, P+ orange-red (fumarprotocetraric acid or succinoprotocetraric acid present) *Variolaria multipunctoides* (Dibben) Lendemer et al.
29. Thallus P- (above substances absent; note that occasionally atranorin gives a P+ yellow reaction when in high concentration) 38

38. Thallus UV+ blue-white (2-*O*-methylperlatolic, alectoronic, divaricatic, perlatolic acid present) 39
39. Thallus distinctly isidiate; isidia robust, tall, coralloid; alectoronic acid present *Protoparmelia isidiata* Diederich, Aptroot & Sérus.
39. Thallus sorediate, pustulose, leprose or with fragile isidioid soredia that are never tall and coralloid 40
40. Thallus leprose, forming extensive continuous colonies; soralia absent; divaricatic acid present *Lepraria hodkinsoniana* Lendemer
40. Thallus continuous or areolate, not forming extensive continuous colonies; soralia, pustulose soralia or isidioid soredia present 41
41. Thallus K+ yellow (atranorin present), sphaerophorin present; rare in the MACP *Haematomma americanum* Staiger & Kalb
41. Thallus K- (atranorin absent); 2-*O*-methylperlatolic acid or perlatolic acid present; common in the MACP 42
42. Thallus green to green brown, forming small rosettes; discrete soralia present; perlatolic acid present; uncommon *Ropalospora viridis* (Tønsberg) Tønsberg
42. Thallus creamy white to blue-gray with a yellowish cast; pustulose soralia or isidioid soredia present; 2-*O*-methylperlatolic acid present; common *Loxospora confusa* Lendemer
38. Thallus UV- 43
43. Thallus sorediate or leprose (composed of granules) 44
44. Thallus scruffy and dirty green in appearance, composed of goniocysts; photobiont micareoid, cells <7 µm in diameter .. 45
45. Micareic acid present (TLC required!) *Micareia prasina* Fr.
45. Methoxymicareic acid present (TLC required!) *Micareia micrococca* (Körb.) Gams ex Coppins
44. Thallus not as above, with soredia or granules; photobiont coccoid, cells >7 µm in diameter 46
46. Thallus leprose, composed entirely of granules and never with a shiny prothallus *Lepraria harrisiana* Lendemer
46. Thallus areolate or continuous, soraliolate 47
47. Thallus K- 48
48. Soralia KC-, not bitter tasting (also C-, P-, and UV-; lacking secondary compounds) .. *Variolaria ophthalmiza* (Nyl.) Darb.
48. Soralia KC+ fleeting purple, bitter tasting (picrolichenic acid present) *Variolaria amara* Ach.
47. Thallus K+ yellow (atranorin present) 49
49. Zeorin present (TLC required!) 50
50. Thallus immersed, with soralia eroding from the substrate *Lecanora nothocaesiella* R.C. Harris & Lendemer
50. Thallus superficial, with coarse pustular soralia *sorediate morph of Brigantiaea leucoxantha*
49. Zeorin absent (TLC required!) 51
51. Caperatic acid present 52
52. Placodiolic acid group substances present; thallus usually with a fibrous white prothallus *Haematomma guyanense* Staiger & Kalb

52. Placodiolic acid absent; thallus without a fibrous white prothallus ***Lecanora* sp.**
51. Caperatic acid absent 53
53. Thallus continuous, creamy white, with discrete soralia; placodiolic acid group substances present.....
..... ***Haematomma guyanense* Staiger & Kalb**
53. Thallus areolate, green, with diffuse to irregular soralia; placodiolic acid absent.....
..... **sterile sorediate crust sp.**
43. Thallus isidiate, blastidiate, or composed of tiny areoles; soredia and granules absent 54
54. On old wood, sand or organic matter 55
55. Thallus composed of tiny, convex, light brown areoles **[*Placynthiella oligotropa* (J.R. Laundon) Coppins & P. James]**
55. Thallus more-or-less a continuous film of minute dark-brown to blackish areoles **[*Placynthiella uliginosa* (Schräd.) Coppins & P. James]**
54. On bark 56
56. Thallus without a distinct white prothallus, areolate with the areoles developing minute globose to +/- flattened blastidia ***Rinodina papillata* H. Magn.**
56. Thallus with a distinct white prothallus, areolate with the areoles developing lobules, proliferations or isidia ... 57
57. Areoles developing lobules or flattened, overlapping marginal proliferations 58
58. Areoles large, squamulose and resembling a foliose lichen, developing lobules.....
..... ***Phyllopsora parvifolia* (Pers.) Müll. Arg.**
58. Areoles small, not squamulose or resembling a foliose lichen, developing minute marginal overlapping proliferations.....
..... ***Phyllopsora confusa* Swinsc. & Krog**
57. Areoles developing coralloid isidia or short globose isidia 59
59. Isidia short, globose; thallus usually pale greenish gray.....
..... ***Phyllopsora confusa* Swinsc. & Krog**
59. Isidia tall, cylindrical to coralloid; thallus distinctly green without a hint of gray.....
..... **[*Phyllopsora corallina* (Eschw.) Müll. Arg.]**

KEY 9. CRUSTOSE PYRENOLICHENS

1. Ascospores hyaline 2
2. Ascospores submuriform or muriform 3
3. Perithecia pale white; thallus scurfy, greenish, composed of gonocysts.....
..... ***Psoroglaena dictyospora* (Orange) H. Harada**
3. Perithecia tan or black; thallus thin and indistinct, not as above 4
4. Perithecia tan, inconspicuous; ostiole apical; ascospores 16–22 × 9–12; thallus concolorous with the substrate, UV- ***Topelia aperiens* P. M. Jørg. & Vězda**
4. Perithecia black, conspicuous; ostiole lateral; ascospores 40–55 × 15–20 µm; thallus gray to white, ecorticate, often patchily UV+ bright yellow (lichexanthone often present)
..... ***Polymeridium proponens* (Nyl.) R.C. Harris**
2. Ascospores transversely septate 5
5. Ascospores 4 or more celled 6

6. Ascospores 4-celled 7
7. Photobiont present 8
 8. Perithecia conspicuous, solitary, naked, and strongly raised above the thallus...
..... *Trypethelium tropicum* (Ach.) Müll. Arg.
 8. Perithecia not conspicuously solitary and raised above the thallus surface 9
 9. Perithecia aggregated in raised pseudostroma; pseudostromata brown and with yellow pigmented tissue in the space between the perithecia *Bathelium carolinianum* (Tuck.) R.C. Harris
 9. Perithecia not aggregated into raised pseudostroma 10
 10. Perithecia black *Polymeridium subcinereum* (Nyl.) R.C. Harris
 10. Perithecia light red-brown to flesh colored 11
 11. Perithecial wall distinctly red in section; ascospores 8 per ascus
..... *Segestria leptalea* (Durieu & Mont.) R.C. Harris
 11. Perithecial wall light brown in section; ascospores many per ascus
..... *Thelopsis rubella* Nyl.
7. Photobiont absent; rarely 4-celled 12
 12. Ascospores $17-20 \times 5-7 \mu\text{m}$ *Mycoporum eschweileri* (Müll. Arg.) R.C. Harris
 12. Ascospores $20-27 \times 6.5-8 \mu\text{m}$ *Mycoporum lacteum* (Ach.) R.C. Harris
6. Ascospores 6 or more celled 13
 13. Perithecia aggregated in conspicuous pseudostromata that often become somewhat raised; thallus bronze or light brown in color *Trypethelium virens* Tuck.
 13. Perithecia solitary, not aggregated in conspicuous pseudostroma 14
 14. Perithecia covered with abundant black apical setae; thallus with minute isidia sparsely present *Trichothelium americanum* Lendemer
 14. Perithecia without black apical setae; thallus not isidiate 15
 15. Ascospores $80-150 \mu\text{m}$ long 16
 16. Ascospores narrow, $3-5 \mu\text{m}$ wide, filiform; perithecial wall dark purple-black in section.....
..... *Pseudosagedia raphidosperma* (Müll. Arg.) R.C. Harris
 16. Ascospores broad, $10-15 \mu\text{m}$ wide, clavate; perithecial wall brown to orange in section *Porina heterospora* (Fink) R.C. Harris
 15. Ascospores $<70 \mu\text{m}$ long 17
 17. Thallus white; ascospores fusiform to ellipsoid, 6-8 celled; rare.....
..... *Polymeridium quinqueseptatum* (Nyl.) R.C. Harris
 17. Thallus gray to brown; ascospores clavate, 8-13 celled; common.....
..... *Pseudosagedia cestrensis* (Tuck.) R.C. Harris
 5. Ascospores 2-celled 18
 18. Ascospores 32 per ascus, $6.5-9 \times 2-3 \mu\text{m}$; parasitic on algal colonies; rarely collected.....
..... *Epigloea pleiospora* Döbbele
 18. Ascospores 8 per ascus, size variable; not parasitic on algal colonies; more common 19
 19. Perithecia arranged in minute compound aggregations that are often flattened; photobiont absent 20
 20. Ascospores $17-20 \times 5-7 \mu\text{m}$ *Mycoporum eschweileri* (Müll. Arg.) R.C. Harris
 20. Ascospores $20-27 \times 6.5-8 \mu\text{m}$ *Mycoporum lacteum* (Ach.) R.C. Harris
 19. Perithecia solitary, not arranged in minute aggregations; photobiont present except in *Arthopyrenia* 21
 21. Ascospores distinctly uniseriate within the ascus, with a median septum 22
 22. Thallus UV+ yellow (lichexanthone present).....
..... *Anisomeridium biformoides* R.C. Harris
 22. Thallus UV- (lichexanthone absent) 23
 23. Ascospores $18-27 \times 9-13 \mu\text{m}$.. *Acrocordia gemmata* (Ach.) A. Massal.
 23. Ascospores $10-18 \times 4-7 \mu\text{m}$
..... *Anisomeridium biforme* (Borrer) R.C. Harris
 21. Ascospores biseriate or irregularly arranged, with a submedian or median septum .. 24
 24. Ascospores $20-30 \times 7-10 \mu\text{m}$; photobiont sparsely present 25
 25. On hardwoods; ascomata superficial.....
..... *Arthopyrenia cinchonae* (Ach.) Müll. Arg.
 25. On *Taxodium*; ascomata immersed .. *Arthopyrenia taxodii* R.C. Harris
 24. Ascospores $<20 \mu\text{m}$ long; photobiont distinctly visible 26

26.	Ascospores with submedian septum; paraphyses branching and anastomosing	27
27.	Ascospores narrowly ellipsoid, 14–20 × 4–6 µm; common	
	 <i>Anisomeridium polypori</i> (Ellis & Everh.) M. E. Barr	
27.	Ascospores broadly ellipsoid, 14–18 × 6–8 µm; rare.....	
	 <i>Anisomeridium anisobolus</i> (Müll. Arg.) Aptroot	
26.	Ascospores with a median septum; paraphyses not branching and anastomosing	28
28.	Ascospores 15–25 × 4–6 µm	<i>Strigula americana</i> R.C. Harris
28.	Ascospores 12–17 × 4–7 µm	
	 <i>Strigula viridiseta</i> (Nyl.) R.C. Harris	
1.	Ascospores brown	29
29.	Ascospores muriform	30
30.	Ascospores 130–225 × 38–50 µm long, 2 per ascus	
	 <i>Anthracotheceum nanum</i> (Zahlbr.) R.C. Harris	
30.	Ascospores <70 µm long, 8 per ascus	31
31.	Ascospores small, 30–42–[53] × 11–15 µm; known from nearby Great Dismal Swamp.....	
	 [<i>Pyrenula thelomorpha</i> Tuck.]	
31.	Ascospores larger, 45–70 × 16–30 µm	32
32.	Perithecia aggregated into groups; ostiole lateral or apical; rare.....	
	 <i>Pyrenula ravenelii</i> (Tuck.) R.C. Harris	
32.	Perithecia solitary; ostiole apical; common	<i>Pyrenula leucostoma</i> Ach.
29.	Ascospores transversely septate	33
33.	Perithecia aggregated and fused into black pseudostroma ..	<i>Pyrenula anomala</i> (Ach.) R.C. Harris
33.	Perithecia solitary, not fused into black pseudostroma	34
34.	Thallus ecorticate, white; perithecia small, black; gestalt resembling an <i>Anisomeridium</i> ...	
	 <i>Pyrenula microcarpa</i> Müll. Arg.	
34.	Thallus corticate, brown or greenish brown; perithecia not as above	35
35.	Ascospores >25 µm long	36
36.	Thallus usually red pigmented, at least near the perithecia; common.....	
	 <i>Pyrenula cruenta</i> (Mont.) Vain.	
36.	Thallus not red pigmented; rare	<i>Pyrenula punctella</i> (Nyl.) Trevis.
35.	Ascospores <25 µm long	37
37.	Ascospores with the terminal lumina directly against the exospores, often citriform (resembling a lemon); perithecia not very large	38
38.	Thallus UV+ yellow (lichexanthone present); often on bases and boles of trees	<i>Pyrenula pseudobufoia</i> (Rehm) R.C. Harris
38.	Thallus UV- (lichexanthone absent); often on the stems of shrubs.....	
	 <i>Pyrenula citriformis</i> R.C. Harris	
37.	Ascospores with the terminal lumina not directly against the exospore, not citriform (not resembling a lemon)	39
39.	Ostiole lateral; thallus thick, mostly covering the perithecia	
	 <i>Pyrenula microtheca</i> R.C. Harris	
39.	Ostiole apical; thallus thin or thick	40
40.	Perithecia small, 0.3–0.4 mm in diameter; thallus thin.....	
	 <i>Pyrenula aspistea</i> Ach.	
40.	Perithecia very large, 0.7–1.2 mm in diameter; thallus thick and shiny ..	41
41.	Hymenium densely interspersed with oil droplets.....	
	 <i>Pyrenula mamillana</i> (Ach.) Trevis.	
41.	Hymenium not interspersed ...	<i>Pyrenula santensis</i> (Nyl.) Müll. Arg.

KEY 10. CRUSTOSE APOTHECIATE LICHENS WITH HYALINE SPORES

1.	Apothecia irregular (e.g., arthonioid) or elongate (lirelliform) in outline	2
2.	Epihymenium or exciple red or orange pigmented, pigments K+ purple or K+ green	3
3.	Pigment red, K+ green (isohypocrellin present); restricted to maritime forests.....	
	 <i>Thalloloma cf. cinnabarinum</i> (Fée) Staiger [collections often without ascospores]	
3.	Pigment red or orange, K+ purple	4

4. Apothecia black, narrowly elongate and lirelliform; exciple carbonized laterally; orange pigment in the epihymenium, pigment K+ purple ***Graphis inversa* R.C. Harris** 5
4. Apothecia red, irregularly shaped but not narrowly elongate and lirelliform 5
 5. Apothecia irregular in shape, with a distinct margin and disc; ascospores clavate, 4-celled, macrocephalic ***Arthonia cinnabarina* (DC.) Wallr.**
 5. Apothecia resembling a heap of mealy red granules; ascospores broadly ellipsoid, 6-celled, not macrocephalic 6
 6. Ascospores present ***Coniarthonia pyrrhula* (Nyl.) Grube**
 6. Ascospores absent .. **sterile material of *Coniarthonia* cf. *pyrrhula* (Nyl.) Grube**
2. Epihymenium or exciple not red or orange pigmented, without pigments that are K+ purple or K+ green ... 7
 7. Apothecia blotchy and fleck-like, irregular in shape but not branching and lirelliform 8
 8. Ascospores transversely septate; photobiont coccoid ***Arthonia albobirescens* Nyl.**
 8. Ascospores submuriform to muriform; photobiont *Trentepohlia* or coccoid 9
 9. Ascospores submuriform, clavate, often +/- bent ***Arthonia interveniens* Nyl.**
 9. Ascospores muriform, ellipsoid, never bent 10
 10. Photobiont coccoid; ascospores remaining hyaline; common ***Arthonia susa* R.C. Harris & Lendemer**
 10. Photobiont *Trentepohlia*; ascospores often turning slightly brownish with age; rare ***Arthonia ruana* A. Massal.**
 7. Apothecia lirelliform, branching or not, but not blotchy and fleck-like 11
 11. Photobiont absent ***Arthonia quintaria* Nyl.**
 11. Photobiont present, *Trentepohlia* or coccoid 12
 12. Exciple carbonized, at least at the apex 13
 13. Disc with a thick, dense white pruina, pruina C+ red (lecanoric acid present) ... ***Dyplotylabia afzelii* (Ach.) A. Massal.**
 13. Disc variably pruinose, but pruina not thick and dense, C- (lecanoric acid absent) .. 14
 14. Lirellae forming dense, carbonized aggregations (pseudostroma) ***Glyphis cicatricosa* Ach.**
 14. Lirellae solitary, not forming dense, carbonized aggregations (pseudostroma) .. 15
 15. Lirellae fissurine, visible as a narrow crack in the thallus; the excipular lips indistinct and poorly developed; exciple weakly carbonized and only at the apex; very rare ***Fissurina subnitidula* (Tuck.) Staiger**
 15. Lirellae not fissurine, with obvious excipular lips that are distinct and well developed; common 16
 16. Exciple completely carbonized 17
 17. Hymenium interspersed with oil droplets ***Graphis desquamescens* Fée**
 17. Hymenium not interspersed 18
 18. Ascospores 12-14 celled; common ***Opegrapha viridis* (Ach.) Behlen & Desberger**
 18. Ascospores 6-celled; infrequent 19
 19. Ascospores narrow, 3-4 µm wide; disc not exposed ***Opegrapha vulgata* Ach.**
 19. Ascospores broad, 5-6 µm wide; disc exposed, often yellow-green pruinose ***Opegrapha varia* Pers.**
 16. Exciple apically or laterally carbonized (i.e., not carbonized under the hypothecium) 20
 20. Exciple carbonized laterally, with the carbonization extending to the base of the hymenium 21
 21. Exciple smooth, entire, not becoming striate 22
 22. Hymenium interspersed with oil droplets 23
 23. Norstictic acid absent (TLC often needed for confirmation) 24
 24. Ascospores 20-40 µm long ***Graphis lineola* Ach.**
 24. Ascospores 40-80 µm long ***Graphis intermedians* Vain.**
 23. Norstictic acid present (TLC often needed for confirmation) 25

25. Disc hidden by the closed lips
 ***Graphis cincta* (Pers.) Aptroot**
25. Disc exposed 26
26. Disc white pruinose
 ***Graphis crebra* Vain.**
26. Disc not pruinose.....
 ***Graphis handelii* Zahlbr.**
22. Hymenium not interspersed 27
27. Disc exposed, white pruinose.....
 ***Graphis scripta* (L.) Ach.**
27. Disc hidden by the closed lips 28
28. Thallus corticate; lips epruinose
 ***Graphis pinicola* Zahlbr.**
28. Thallus at least partially ecorticate;
 lips lightly white pruinose.....
 ***Graphis furcata* Fée**
21. Exciple ridged, becoming striate 29
29. Ascospores $30\text{--}65 \times 7\text{--}12 \mu\text{m}$
 ***Graphis striatula* (Ach.) Spreng.**
29. Ascospores $15\text{--}45 \times 6\text{--}9 \mu\text{m}$ 30
30. Lirellae long, abundantly branched
 ***Graphis duplicata* Ach.**
30. Lirellae short, little branched
 ***Graphis tenella* Ach.**
20. Exciple carbonized only at the apex, with the carbonization
 never extending more than one-third of the way to the base
 of the hymenium 31
31. Exciple ridged, striate ***Graphis endoxantha* Nyl.**
31. Exciple smooth, entire, not striate
 ***Graphis vittata* Müll. Arg.**
12. Exciple not carbonized 32
32. Thallus (test the lips) P+ yellow or orange (norstictic, psoromic or stictic acid
 present) 33
33. Thallus P+ orange (concentrated on the lips; stictic acid present); very rare
 ***Acanthothecis leucoxanthoides* Lendemer**
33. Thallus P+ yellow (norstictic or psoromic acid present); common 34
34. Thallus K+ yellow turning red, producing norstictic acid crystals
 (norstictic acid present); paraphyses ornamented with apical spines;
 rare ***Acanthothecis mosquitensis* (Tuck.) E.A. Tripp & Lendemer**
34. Thallus K- (psoromic acid present); paraphyses not ornamented with
 apical spines 35
35. Apothecia fissurine, resembling mealy cracks of the thallus;
 ascospores muriform; throughout the DRBH.....
 ***Fissurina columbina* (Tuck.) Staiger**
35. Apothecia lecanorine, resembling irregularly shaped *Lecanora*;
 ascospores transversely septate; coastal maritime forests
 ***Enterographa anguinella* (Nyl.) Redinger**
32. Thallus P- 36
36. Apothecia and thallus C+ pink in section (gyrophoric acid present)
 ***Arthonia anglica* Coppins**
36. Apothecia and thallus C- in section (gyrophoric acid absent) 37
37. Thallus UV+ bright yellow, though often patchily so (lichexanthone
 present) ***Thalloloma hypoleptum* (Nyl.) Staiger**
37. Thallus UV- (lichexanthone absent) 38
38. Lirellae fissurine, resembling a crack in the substrate 39
39. Thallus blue-green to green-brown, thick and shiny 40
40. Lirellae without distinct swollen lips; rare.....
 ***Fissurina incrustans* Fée**
40. Lirellae with distinct swollen lips 41

41. Lirellae more-or-less immersed in the substrate; ascospores 4-celled; common.....
..... ***Fissurina insidiosa* C. Knight & Mitt.**
41. Lirellae more-or-less sessile; ascospores submuriform; rare
..... ***Fissurina scolecitis* (Tuck.) Lendemer**
39. Thallus white or gray to blue-green, thin and often dull 42
42. Ascospores submuriform to muriform 43
43. Ascospores large, 1 per ascus, 1-, 80–100 µm long; thallus white, often flaky and appearing sorediate or schizidiolate.....
..... ***Fissurina cypressi* (Müll. Arg.) Lendemer**
43. Ascospores small, 6-8 per ascus, 1+ violet, 15–30 µm long; thallus blue-gray to white, not flaky and appearing to have lichenized diaspores
***Fissurina alligatorensis* Lendemer & R.C. Harris**
42. Ascospores transversely septate 44
- 44 Lirellae with white, crumbling margins; paraphyses with apical ornamentation.....
..... ***Acanthothecis paucispora* Lendemer & R.C. Harris**
44. Lirellae slit-like and not with crumbling margins; paraphyses not ornamented at the tips 45
45. Exciple apically carbonized, the carbonization visible as a dark area near the crack exposing the disc; rare.....
..... ***Fissurina subnitidula* (Tuck.) Staiger**
45. Exciple not carbonized; common.....
***Fissurina illiterata* (R.C. Harris) Lendemer**
38. Lirellae not as above 46
46. Ascospores muriform; photobiont coccoid
..... ***Arthonia susa* R.C. Harris & Lendemer**
46. Ascospores transversely septate; photobiont *Trentepohlia* or coccoid 47
47. Ascospores 6-celled, with the end two cells enlarged and the middle four cells distinctly narrowed; photobiont *Trentepohlia*.....
..... ***Arthonia rubella* (Fée) Nyl.**
47. Ascospores 8-12-celled, cells more-or-less equal in size; photobiont coccoid ***Arthonia albobirescens* Nyl.**
1. Apothecia circular in outline, regular in shape, neither irregular nor elongate 48
48. Ascospores muriform 49
49. Apothecia bright orange, discoid, not opening through a pore
..... ***Brigantiaea leucoxantha* (Spreng.) R. Sant. & Hafellner**
49. Apothecia gray or brown, thelotremoid, opening through a pore 50
50. Exciple carbonized, carbonized columella often present 51
51. Thallus P+ yellow (subpsoromic acid present); rare in DRBH.....
..... ***Ocellularia praestans* (Müll. Arg.) Hale**
51. Thallus P- (subpsoromic acid absent); common in DRBH
..... ***Ocellularia sanfordiana* (Zahlbr.) Hale**
50. Exciple not carbonized, carbonized columella absent 52
52. Ascospores 1 per ascus, >100 µm long, often turning brownish at maturity
..... ***Thelotrema monospermum* R.C. Harris**
52. Ascospores 6-8 per ascus, 20–90 µm long, not turning brown at maturity 53
53. Ascospores small, obtuse ellipsoid, 20–40 µm long; apothecia tiny, resembling a *Stictis* ***Thelotrema defectum* R.C. Harris**
53. Ascospores large, ellipsoid, 60–90 µm long; apothecia large, not resembling a *Stictis* ***Thelotrema adjectum* Nyl.**
48. Ascospores simple or transversely septate 54
54. Ascospores simple 55
55. Asci polysporous; ascospores many per ascus (>100), small globose or ellipsoid 56

56. Thallus yellow, K+ purple *Piccolia nannaria* (Tuck.) Lendemer & Beeching
56. Thallus indistinct or gray-brown, K- 57
57. Apothecia immersed, not lecanorine, resembling a white crater and appearing to open through a pore, K- *Ramonia microspora* Vězda
57. Apothecia sessile not immersed in the substrate 58
58. Apothecia lecanorine, with a distinct thalline margin, medulla of the margin KC+ purple; common *Maronea polyphaea* H. Magn.
58. Apothecia biatorine, without a thalline margin, margin KC-; rare *Albemarlea pamlicoensis* Lendemer & R.C. Harris
55. Asci not polysporous, ascospores 8 per ascus or fewer, size and shape various 59
59. Apothecia contained in dome-shaped warts, tipped with an ostiole (*Pertusaria*) 60
60. Medulla K+ yellow turning red, producing norstictic acid crystals (norstictic acid present) 61
61. Ascospores 8 per ascus *Pertusaria propinqua* Müll. Arg.
61. Ascospores 2 per ascus *Pertusaria neoscotica* I.M. Lamb
60. Medulla K- or K+ yellow, but not K+ yellow turning red (norstictic acid absent) ... 62
62. Thallus UV+ bright yellow (lichexanthone present) *Pertusaria paratuberculifera* Dibben
62. Thallus UV+ orange, UV+ dull pink, or UV- 63
63. Ascospores 8 per ascus; ostiolar area usually yellow 64
64. Medulla P+ orange (stictic acid present); ostiole typically raised, resembling a nipple *Pertusaria texana* Müll. Arg.
64. Medulla P- (variolaric acid present); ostiole typically depressed, not resembling a nipple *Pertusaria epixantha* R.C. Harris
63. Ascospores 2-4 per ascus; ostiolar area usually not yellow 65
65. Thallus UV+ bright orange (thiophanic acid present) *Pertusaria pustulata* (Ach.) Duby
65. Thallus UV- or UV+ dull pink or orange (thiophaninic acid absent) .. 66
66. Medulla P+ orange or red (succinoprotocetraric or stictic acid present) 67
67. Ascospores 2 per ascus; warts compound, flattened; succinoprotocetraric acid present *Pertusaria subpertusa* Brodo
67. Ascospores (2-)4 per ascus; warts simple to compound, hemispherical; stictic acid present *Pertusaria tetrathalamia* (Fée) Nyl.
66. Medulla P- (succinoprotocetraric or stictic acid absent) 68
68. Hymenium densely dispersed with oil droplets; warts usually sessile *Pertusaria sinusmexicani* Dibben
68. Hymenium not interspersed; warts usually immersed ... *Pertusaria obruta* R.C. Harris
59. Apothecia not contained in dome-shaped warts, not tipped with an ostiole 69
69. Apothecia lecanorine, with a distinct thalline margin (note that *Variolaria* species with usually sterile, convex, densely pruinose apothecia that resemble soralia also key out here) 70
70. Margin and disc of apothecia C+ pink-red *Ochrolechia africana* Vain.
70. Margin and disc of apothecia C- or C+ yellow-orange 71
71. Epihymenium C+ yellow-orange (xanthonenes present) 72
72. Disc densely white pruinose; apothecia K+ yellow turning red (norstictic acid) in section *Lecanora subpallens* Zahlbr.
72. Disc lightly to densely orange-yellow pruinose; apothecia K+ yellowish (atranorin) in section .. *Lecanora louisianae* B. de Lesd.
71. Epihymenium C- (xanthonenes absent) 73
73. Discs densely white pruinose 74
74. Ascospores 8 per ascus, small, <20 µm long *Lecanora caesiorubella* Ach. subsp. *glaucomodes*
74. Ascospores 1-2 per ascus, large, >50 µm long 75
75. Pruina P+ orange or red (haemathamnolic, succino-protocetraric, and thamnolic acid present) 76

76. Thallus UV-; pruina K- or K+ dirty yellowish-brown **Variolaria multipunctoides (Dibben) Lendemer et al.**
76. Thallus UV+ bright yellow (lichexanthone present); pruina K+ intense yellow turning brown or reddish-brown 77
77. Pruina K+ intense yellow almost instantly turning a dark reddish-brown; common
.. **Variolaria commutata (Mull. Arg.) ined.**
77. Pruina K+ intense yellow slowly turning dirty brown; rare
..... **Variolaria trachythallina (Erichsen) Lendemer et al.**
75. Pruina P- (other substances present) 78
78. Pruina K+ lavender (hypothamnolic acid present)
..... **Variolaria hypothamnolica (Dibben) ined.**
78. Pruina K- (hypothamnolic acid absent) 79
79. Pruina KC+ violet (picrolichenic acid present) **Variolaria amara Ach.**
79. Pruina KC- (picrolichenic acid absent)
..... **Variolaria ophthalmiza (Nyl.) Darb.**
73. Discs not epruinose or sparsely pruinose 80
80. Thallus green; apothecial disc greenish-yellow to intense yellow (usnic acid present) 81
81. Apothecial margin ecorticate, granular
..... **Lecanora strobilina (Spreng.) Kieff.**
81. Apothecial margin corticate, smooth
..... **Lecanora cupressi Tuck.**
80. Thallus gray; apothecial disc reddish-brown to purple-brown (usnic acid absent) 82
82. Apothecial margins ecorticate, stark white contrasting against the disc **Lecanora imshaugii Brodo**
82. Apothecial margins corticate, not as above 83
83. Disc dark purple-black; hymenium purple; medulla UV+ blue-white (aleatoronic acid present) ...
..... **Tephromela atra (Huds.) Hafellner**
83. Disc reddish-brown; hymenium hyaline; medulla UV- (aleatoronic acid absent) 84
84. Epithymenium P+ orange-red (pannarin present); infrequent in inland swamps
..... **Lecanora cinereofusca H. Magn.**
84. Epithymenium P- (pannarin absent); common throughout DRBH 85
85. Disc epruinose; epithymenium with fine POL+ crystals; very common ...
.. **Lecanora hybocarpa (Tuck.) Brodo (when in doubt, choose this one)**
85. Disc weakly white pruinose; epithymenium with coarse POL+ crystals; rare
..... **Lecanora chlarotera Nyl.**
69. Apothecia not lecanorine, without a distinct thalline margin 86
86. Apothecia bright red, K+ intense red-purple (russulone present)
..... **Ramboldia russula (Ach.) Kalb, Lumbsch & Elix**
86. Apothecia tan to brown, never bright red and K+ intense purple (russulone absent) 87
87. Thallus KC+ yellow-orange, UV+ orange (xanthones present) 88
88. Thallus granular, leprose; apothecia dark, blackish, epruinose ..
..... **Pyrrospora sp.**
88. Thallus continuous, smooth to verruculose; apothecia reddish to tan, highly variable in color, frequently pruinose
..... **Pyrrospora varians (Ach.) R.C. Harris**

87. Thallus KC-, UV- (xanthonenes absent) 89
89. Thallus scurfy, green, granular, composed of goniocysts; apothecia pallid or tan 90
90. Micareic acid present [TLC required] *Micareia prasina* Fr.
90. Methoxymicareic acid present [TLC required]
..... *Micareia micrococca* (Körb.) Gams ex Coppins
89. Thallus thin and indistinct, continuous or areolate, but not scurfy green and granular 91
91. Thallus not evident; apothecia brownish-red; sporodochia absent; restricted to conifer wood in maritime forests
..... *Aggyrium rufum* (Pers.) Fr.
91. Thallus evident, areolate or continuous; apothecia dark brown-black; sporodochia usually present; on old large logs of conifers in swampy habitats and maritime forests
..... *Xyleborus nigricans* R.C. Harris & Lendemer
54. Ascospores transversely septate 92
92. Apothecial disc red or yellow-orange pigmented, pigment K+ purple, pink or green 93
93. Thallus on concrete; apothecia yellow orange *Caloplaca feracissima* H. Magn.
93. Thallus on bark or wood 94
94. Apothecia orange; ascospores polarilocular, with thickened walls and angular lumina *Caloplaca flavorubescens* (With.) J.R. Laundon
94. Apothecia red; ascospores multi-celled with regular septa, not polarilocular 95
95. Apothecia not lecanorine, erumpent, K+ green, often with remains of small bark flaps near the margins; rare and restricted to maritime forests
..... *Thallotoma cf. cinnabarinum* (Fée) Staiger
95. Apothecia lecanorine, not erumpent, K+ red-pink or purple, always without bark flaps; common throughout the DRBH 96
96. Epihymenium K+ red-pink (russulone present); medulla UV+ blue-white (sphaerophorin present); restricted to maritime forests
..... *Haematomma persoonii* (Fée) A. Massal.
96. Epihymenium K+ purple (haematommone present); medulla UV- (sphaerophorin absent); primary in inland swamps 97
97. Placodiolic acid present (TLC required); common
..... *Haematomma accolens* (Stirt.) Hillmann
97. Pseudoplacodiolic acid and isopseudoplacodiolic acid present (TLC required); rare *Haematomma flexuosum* Hillmann
92. Apothecial disc not red or yellow-orange pigmented or the pigment, if present, not K+ purple or pink 98
98. Apothecia large, erumpent, with large ragged bark flaps along the margins; disc pruinose
..... *Thelotrema dilatatum* (Müll. Arg.) Hale
98. Apothecia not large and erumpent with large ragged bark flaps 99
99. Apothecia thelotremoid, and opening through a distinct pore 100
100. Ascospores large, >100 µm long; medulla C+ pink
..... *Ocellularia americana* Hale
100. Ascospores small, <50 µm long; medulla C- 101
101. Thallus ecorticate, poorly developed; common
..... *Thelotrema subtile* Tuck. (when in doubt, choose this one)
101. Thallus corticate, well-developed; rare *Thelotrema lathraeum* Tuck.
99. Apothecia discoid, not opening through a pore 102
102. Ascospores 2-celled 103
103. Photobiont *Trentepohlia*; apothecia yellowish-orange
..... *Coenogonium luteum* (Dicks.) Kalb & Lücking
103. Photobiont coccoid; apothecia reddish brown or pale to tan 104
104. Ascospores polarilocular, with thickened walls and angular lumina *Caloplaca camptidia* (Tuck.) Zahlbr.
104. Ascospores not polarilocular, with regular septa 105
105. Apothecia distinctly bicolored, with a white margin contrasting against the dark blue-black disc; rare
..... *Megalaria alligatorensis* Lendemer & R.C. Harris

105. Apothecia not bicolored, the margin (if present), concolorous with the disc; common 106
106. Apothecia reddish-brown; thallus smooth or thin areolate
 *Catinaria atropurpurea* (Schaer.) Vězda & Poelt
106. Apothecia tan or pallid; thallus scurfy, green, granular, composed of goniocysts 107
107. Apothecia raised, strongly stipitate, with a roughened surface due to the protrusion of paraphyses and asci from the hymenium; infrequent
 *Vezdaea leprosa* (P. James) Vězda
107. Apothecia not raised and stipitate, with a smooth surface; common 108
108. Micareic acid present [TLC required]
 *Micareia prasina* Fr.
108. Methoxymicareic acid present [TLC required] *Micareia micrococca* (Körb.)
 Gams ex Coppins
102. Ascospores >2-celled 109
109. Ascospores fragile, readily fragmenting into part spores 110
110. Ascospores <30 µm long, 4-6 celled; on *Taxodium*; very rare...
 *Bactrospora brevispora* R.C. Harris
110. Ascospores >30 µm long, 10-20 celled; on various substrates 111
111. Ascospores 35–50 × 3 µm; common
 *Bactrospora carolinensis* (Ellis & Everh.) R.C. Harris
111. Ascospores 80–90 × 7–10 µm; infrequent
 *Bactrospora lamprospora* (Nyl.) Lendemer
109. Ascospores not fragile, typically remaining intact and not forming part spores 112
112. Ascospores needle shaped, <3 µm wide 113
113. Ascospores short, <20 µm long 114
114. Pycnidia stipitate; thallus UV+ blue-white (lobaric acid present) and usually P+ orange-red (fumarprotocetraric acid present); common on *Pinus*
 *Micareia neostipitata* Coppins & P. May
114. Pycnidia not stipitate; thallus UV- and P- (lobaric acid and fumarprotocetraric acid absent); rare and restricted to *Chamaecyparis* and *Taxodium*
 *Micareia chlorosticta* (Tuck.) R.C. Harris
113. Ascospores longer, >20 µm long 115
115. On concrete *Bacidina egenula* (Nyl.) Vezda
115. On bark 116
116. Hypothecium dark brown 117
117. Epithymenium K+ purple; hypothecium orange-brown pigmented, pigment K-
 *Bacidia helicospora* S. Ekman
117. Epithymenium K-; hypothecium brown pigmented, pigment K- or K+ rose-red 118
118. Brown pigmented portions of the exciple diffuse K+ rose-red; rare
 *Bacidia diffracta* S. Ekman
118. Brown portions of the exciple K- or K+ more intense brown-purple; common .. 119
119. Epithymenium blue-green pigmented; hypothecium and exciple dark purple-brown pigmented; apothecia dark black in color...
 *Bacidia schweinitzii*
 (Fr. ex Tuck.) A. Schneid.

119. Epithymenium hyaline; hypothecium and exciple reddish-brown pigmented; apothecia reddish brown in color.....
 *Bacidia schweinitzii*
 (Fr. ex Tuck.) A. Schneid. (brown color form)
116. Hypothecium pale yellowish to hyaline 120
120. Epithymenium with pigment forming distinct caps over the paraphyses; primarily coastal
 ... *Bacidia heterochroa* (Müll. Arg.) Zahlbr.
120. Hymenium with evenly dispersed pigment, or not pigmented 121
121. Apothecia dark brown; epithymenium K+ purple.....
 *Bacidia helicospira* S. Ekman
121. Apothecia pale, pallid; epithymenium K- *Bacidina* spp. not treated here
112. Ascospores fusiform, ellipsoid or otherwise, but >3 µm wide and not needle shaped 122
122. Margins of apothecia fuzzy, white, byssoid 123
123. Hypothecium pale; apothecial discs pale yellow, thallus UV+ dull orange (xanthones) present)
 *Byssoloma meadii* (Tuck.) S. Ekman
123. Hypothecium dark; apothecial discs dark blue-gray or dark brown, thallus UV-.....
 *Byssoloma leucoblepharum* (Nyl.) Vain.
122. Margins of apothecia smooth, not fuzzy and byssoid 124
124. Apothecial discs yellow or greenish pruinose.....
 *Cresponea flava* (Vain.) Egea & Torrente
124. Apothecial discs epruinose or brown pruinose 125
125. Apothecia resembling tiny black urns; discs brown pruinose
 *Glyphis scyphulifera* (Ach.) Staiger
125. Apothecia not resembling tiny black urns; discs epruinose 126
126. Apothecial discs white, C+ pink in section (gyrophoric acid present); restricted to inland swamps *Micarea peliocarpa*
 (Anzi) Coppins & R. Sant.
126. Apothecial discs dark brown, C- (gyrophoric acid absent); mostly in coastal maritime forests 127
127. Ascospores 4-celled; thallus thick, apothecia immersed in the thallus ...
 ... *Mazosia carnea* (Eckfeldt) Aptroot & M. Cáceres
127. Ascospores 6-celled; thallus thin, apothecial sessile
 *Schismatomma* cf. *rappii*
 (Zahlbr.) R.C. Harris

KEY 11. CRUSTOSE APOTHECIATE LICHENS WITH BROWN SPORES

1. Apothecia elongate in outline, lirelliform 2
2. Ascospores transversely septate, 4-10 celled 3
3. Ascospores 6-10 celled 4
4. Lirellae distinctly elongate, often weakly branched, not erumpent and surrounded by ragged bark flaps; ascospores 6-celled [*Phaeographis/Leiorreuma* sp.]
4. Lirellae circular to distinctly elongate, strongly erumpent and often surrounded by ragged bark flaps; ascospores 6-10 celled 5

5. Coastal maritime forests; lirellae circular *Phaeographis lobata* (Eschw.) Müll. Arg.
5. Inland swamps, often in the canopy; lirellae elongate.....
..... *Phaeographis erumpens* (Nyl.) Müll. Arg.
3. Ascospores 4-celled 6
6. Hymenium not inspersioned; medulla P+ yellow or orange (norstictic and/or stictic acid present);
exciple weakly carbonized at the apex, if at all.....
..... *Phaeographis brasiliensis* (A. Massal.) Kalb & Matthes-Leicht
6. Hymenium inspersioned with oil droplets; medulla P- (norstictic/stictic acid absent); exciple
variably carbonized 7
7. Lirellae forming aggregations (pseudostroma) of variable branching density where the
hymenium becomes cracked and divided; pseudostromata surrounded by distinctly
whitish tissue that differs markedly in color and texture from the surrounding thallus
..... *Sarcographa tricola* (Ach.) Müll. Arg.
7. Lirellae not forming aggregations (pseudostroma) that are surrounded by distinctly
whitish tissue that differs markedly in color and texture from the surrounding thallus ... 8
8. Exciple apically carbonized; rare in DRBH
..... *Phaeographis inusta* (Ach.) Müll. Arg.
8. Exciple completely carbonized, with the carbonization often penetrating into the
hypotheccium; common in DRBH *Leiorreuma sericeum* (Eschw.) Staiger
2. Ascospores submuriform to muriform 9
9. Ascospores submuriform, 25–30 × 10–12 µm; lirellae elongate, often branching, with a distinct
white thalline margin, not erumpent; throughout DRBH .. *Leiorreuma explicans* (Fink) Lendemer
9. Ascospores muriform, 90–150 × 25–35 µm; lirellae circular, never branching, erumpent and
surrounded by ragged bark flaps; restricted to mature maritime forests.....
..... *Phaeographis oricola* Lendemer & R.C. Harris
1. Apothecia circular in outline 10
10. Ascospores muriform 11
11. Apothecia immersed, opening through a pore, not erumpent surrounded by ragged bark flaps;
ascospores 100–150 × 25–30 µm; restricted to inland swamps
..... *Thelotrema monospermum* R.C. Harris
11. Apothecia immersed, but not opening through a pore, strongly erumpent and surrounded by ragged
bark flaps; ascospores 90–150 × 25–35 µm; restricted mature maritime forests.....
..... *Phaeographis oricola* Lendemer & R.C. Harris
10. Ascospores transversely septate, < 90 × 20 µm 12
12. Ascospores 4–10 celled 13
13. Ascospores 4-celled; hymenium not inspersioned; apothecia lecideine, small; thallus composed
of minute green areoles; inland swamps *Buellia vernicoma* (Tuck.) Tuck.
13. Ascospores 6–10 celled; hymenium inspersioned with oil droplets; apothecia erumpent, large;
thallus a thick brown continuous crust; maritime forests.....
..... *Phaeographis lobata* (Eschw.) Müll. Arg.
12. Ascospores 2-celled 14
14. Hypotheccium hyaline 15
15. Ascospores (18–)24–27(–34) × (11–)13–15(–17) µm; rare
..... *Rinodina dolichospora* Malme
15. Ascospores (12–)17–18(–23) × (6–)8–9(–10) µm; common.....
..... *Rinodina maculans* Müll. Arg.
14. Hypotheccium brown 16
16. Ascospores 16–32 per ascus *Amandinea polyspora* (Willey) E. Lay & P. May
16. Ascospores 8 or fewer per ascus 17
17. Thallus K+ yellow turning red, with norstictic acid crystals in section (norstictic acid
present) 18
18. Ascospores 10–15 × 5–7 µm; typically on trunks at base and boles
..... *Buellia stillingiana* J. Steiner
18. Ascospores 16–23 × 6–10 µm; typically on branches in the canopy or on small
stems of shrubs 19
19. Ascospores with thickened walls and angular lumina; on *Chamaecy-*
paris; rare *Buellia imshaugiana* R.C. Harris
19. Ascospores not with thickened walls and angular lumina; on diverse
substrates including *Chamaecyparis*; common
..... *Buellia curtisii* (Tuck.) Imshaug

17. Thallus K- or K+ yellowish, but not turning red with norstictic acid crystals in section (norstictic acid absent) 20
20. Apothecial section with K+ pink or orange-red pigments in the epihymenium or exciple 21
 21. Photobiont present; thallus composed of minute green areoles; epihymenium K+ fleeting pink; exciple K- ***Buellia elizae* (Tuck.) Tuck.**
 21. Photobiont absent; thallus not evident; epihymenium K-; exciple K+ strong orange-red **gen et sp. nov. aff. *Schrakia***
20. Apothecial section without K+ pink or orange red pigments in the epihymenium or exciple 22
 22. Thallus composed of minute green areoles containing bright pink pigment (pigment often difficult to observe without a compound microscope), P+ yellow (baeomycesic acid present)..... ***Gassicurtia acidobaeomyceta* Marbach**
22. Thallus not as above, without a pigment, P- 23
 23. Ascospores with thickened walls and angular lumina; restricted to maritime forests ***Hafellia* sp.**
 23. Ascospores without thickened walls and angular lumina; distribution various 24
 24. Ascospores <14 µm long, smooth, not ornamented 25
 25. Apothecia erumpent, retaining a thalline margin, at least when young; coastal maritime forests..... ***Amandinea milliaria* (Tuck.) P. May & Sheard**
 25. Apothecia not erumpent, without a thalline margin; throughout..... ***Amandinea punctata* (Hoffm.) Coppins & Scheid.**
 24. Ascospores >14 µm long, rough, ornamented 27
 26. Thallus barely evident, always lacking soralia; ascospores 15–18 × 10–12 µm; restricted to maritime forests ***Amandinea langloisii* Marbach**
 26. Thallus evident, composed of thin green areoles, often with a few sparse yellow soralia at the margins; ascospores 14–19 × 9–12 µm; common throughout DRBH **rare abundantly fertile forms of *Buellia wheeleri* R.C. Harris**