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 haematommatum sp. nov. (on Haematomma persoonii), Megalaria alligatorensis sp. nov., Minutoexcipula minitoeccipula 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 89,091 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, LeGrand 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
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 Newman 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
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

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.
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 × collector × 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 pre-study 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 Elenssohn 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 (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
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.

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<tr>
<th>This Study</th>
<th>Schafale &amp; Weakley (1990)</th>
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<tr>
<td>Peatland (Pocosin)</td>
<td>Natural Community</td>
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<td>Palustrine system</td>
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<td>High pocosin</td>
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<td>Pond pine woodland</td>
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<td>Peatland (Atlantic White Cedar)</td>
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<td>Upland (Inland)</td>
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<td>Upland (Coastal)</td>
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<td>Marshes/Nonforested Wetlands</td>
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<td>Tidal freshwater marsh</td>
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<td>Swamps</td>
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<td>Nonriverine swamp forest</td>
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<td>Esturine fringe loblolly pine forest</td>
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<td>Tidal cypress-gum swamp</td>
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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 chamaeyparicola* 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 & R.C. Harris (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 subsistence, 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 Phaeophys 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 \( \geq 80 \) 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 \( \pm 48 \) 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.
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 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
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-

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### 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Vouchers</th>
<th>Occurrences</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>%</td>
</tr>
<tr>
<td><strong>Growth Form</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crustose</td>
<td>272</td>
<td>71</td>
</tr>
<tr>
<td>Foliose</td>
<td>80</td>
<td>21</td>
</tr>
<tr>
<td>Fruticose</td>
<td>34</td>
<td>9</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>386</strong></td>
<td>4,803</td>
</tr>
<tr>
<td><strong>Photobiont</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyanobacteria</td>
<td>17</td>
<td>4</td>
</tr>
<tr>
<td>Lichenicolous</td>
<td>34</td>
<td>9</td>
</tr>
<tr>
<td>Other Green Algae</td>
<td>212</td>
<td>55</td>
</tr>
<tr>
<td>Photobiont absent</td>
<td>15</td>
<td>4</td>
</tr>
<tr>
<td>Trentepohlia</td>
<td>108</td>
<td>28</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>386</strong></td>
<td><strong>4,803</strong></td>
</tr>
<tr>
<td><strong>Reproductive Mode</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fungal Asexual</td>
<td>15</td>
<td>4</td>
</tr>
<tr>
<td>Lichenized Asexual</td>
<td>113</td>
<td>30</td>
</tr>
<tr>
<td>Sexual</td>
<td>258</td>
<td>68</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>386</strong></td>
<td><strong>4,803</strong></td>
</tr>
</tbody>
</table>
raria 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. subintectorium (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 $\bar{x} = 0.35 \pm 0.12$), 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 $\sim 60\%$ similar. This relatively higher degree of similarity is likely 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
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 summarizing 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. accoens*, *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,

<p>| Table 4. Overlap between species assemblages collected by three team members at 24 sites in the Dare Regional Biodiversity Hotspot expressed as the average ± SD of Sørensen similarity values obtained from all possible pairwise comparisons (n = 24 comparisons per collector pair). |
|-----------------------------------|-----------------|-----------------|-----------------|</p>
<table>
<thead>
<tr>
<th></th>
<th>Buck</th>
<th>Harris</th>
<th>Lendemer</th>
</tr>
</thead>
<tbody>
<tr>
<td>Buck</td>
<td>—</td>
<td>0.180 ± 0.093</td>
<td>—</td>
</tr>
<tr>
<td>Harris</td>
<td>0.170 ± 0.087</td>
<td>0.318 ± 0.093</td>
<td>—</td>
</tr>
<tr>
<td>Lendemer</td>
<td>0.170 ± 0.087</td>
<td>0.318 ± 0.093</td>
<td>—</td>
</tr>
</tbody>
</table>

*Figure 7.* Graphs summarizing the number of vouchers (left) and number occurrences (right) for species in the Dare Regional Biodiversity Hotspot.
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 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, $0.35 \pm 0.11$ 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. submarginalae 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 Buellia tryptetheli 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. sculeotis), Ocellularia s.l. (O. americana, O. praestans, O. sandforiana), and Pyrenula (P. anomalae, 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. Asterothryium 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 harrisiaina, Micarea pelioca, Phaeocalicium polyoporaeum, and Ropa-lospora viridis. Many of the 230 taxa (66%) found in the DRBH that occur both north and
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 macrolichens and microlichens groups (Brodo 1968, Moore 1968,

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**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. (white circles). 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.
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 haematommatum* 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, sylviculture) 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, diaspore...
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., Hodkinson 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.

ACKNOWLEDGMENTS This study and the authors were supported by NSF DEB-1145511 (to principal investigators J.C. Lendemer and R.C. Harris). We thank Erin Tripp for helpful discussion and encouragement in preparing the descriptive statistics portion of the manuscript. We thank Josef Hafellner and Toby Spribille for discussion of Albemarlea. We thank the following for their companionship in the field: J.L. Allen, W.R. Buck, T. McMullin, E. Tripp, and all the participants of the 2014 Tuckerman Workshop. We thank the staff of the Tranquil House Inn (Manteo, North Carolina) for their hospitality. The Coastal Studies Institute of the University of North Carolina (Wanchese, North Carolina) provided important logistical support. The staff and land managers of Alligator River National Wildlife Refuge, Bull Neck Swamp North Carolina State University Forest, Cape Hatteras National Seashore, Cape Lookout National Seashore, North Carolina National Estuarine Research Reserves, North Carolina Wildlife, Pine Island Audubon Sanctuary, Pocosin Lakes National Wildlife Refuge, and Tyrrell County Palmetto-Peartree Preserve provided access to protected areas and facilitating the issuing of permits to allow our work.

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

Albemarlea Lendemer & R.C. Harris gen. nov.

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 macrocarpospores, 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.
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
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 Fuscideaceae 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 et al. 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 Fuscideaceae 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 ascosporas, conspicuous macrosporadica producing hyaline, narrowly fusiform, two-celled macroconidia, and inconspicuous micropycnidiadica 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 Symlocos–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 μm, hyaline, not inspersed; **paraphyses** slender, not or little branched, not distinctly expanded at the apices, **hymenium** 100- to 230-μm thick, hyaline, inspersed with oil droplets; **exciple** 50-70-μm 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 × 20–40 μm; **ascosporas** ellipsoid, simple, hyaline, many per ascus, thin walled, ca. 3.8–4.8 × 1.9–2.3 μm. **Pyecnidia** of two types: **macropycnidiad** abundant, conspicuous, raised above the thallus surface, walls reddish-brown, 250–300 × 50–70 μm; **macroconidia** forming a distinct white mass billowing out of the ostiole, narrowly fusiform, hyaline, one septate (rarely becoming two septate), 7.7–9.7 × 1.6–1.9 μm; **micropycnidia** sparse(?), inconspicuous, immersed in the thallus, walls hyaline, but becoming brown pigmented near the ostiole, 100–150 × 50–70 μm; **microconidia** rod-shaped, weakly to strongly bent and curved, simple, hyaline, 8–9.5 × 1.0–1.5 μm. **Photobiont** a coccoid green alga, cells 7–10 μm 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., Dictyocatenulata alba, Xyleborus nigricans), because the macrosporadica 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 ± confluent groups. *Ascospores* two (three) septate, macrocephalic, 13–14.7–16.7 × 5.2–6.0–7.5 \(\mu\)m, halonate. *Pyclenia* (seen only once), immersed, ± globose, with pale yellow brown wall, ca. 60-\(\mu\)m across; *conidia* bacillar, hyaline, 3.5–5 × 1.2–1.5 \(\mu\)m.

**Etymology.** – The epithet “agelastica” (=dispersed 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\(^-\), K\(^+\), \(P\), 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 other states in eastern North America failed to reveal any additional material of *A. agelastica*. 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-\(\mu\)m across, 100-\(\mu\)m high; *epihymenium* brown; *hymenium* colorless; *hymenial* gel I\(^+\) orangish, K\(^+\) blue; *paraphyses* slender, weakly expanded at tips with brown caps; *hypothecium* colorless. *Asci* initially broadly clavate, more elongate at maturity, with tiny K\(^+\) apical ring, with 8 spores; *ascospores* colorless becoming brown and warted in age, two (three) septate, macrocephalic, 13–14.7–16.7 × 5.2–6.0–7.5 \(\mu\)m, halonate. *Pyclenia* (seen only once), immersed, ± globose, with pale yellow brown wall, ca. 60-\(\mu\)m across; *conidia* bacillar, hyaline, 3.5–5 × 1.2–1.5 \(\mu\)m.

**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°48'12"N 76°06'30"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).
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. carpinea* (L.)

![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 fuchsins (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.](image-url)
Vainio and L. pallida (Schreb.) Rabenh. (Triebel 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 (Triebel et al. 1991).

Additional specimens examined (all on thalli of Lecanora louisiana). – 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 Higgsport 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 epihyme-
nium that is $K^+$ magenta (vs. $K^+$ dull olive) and an $I^+$ blue (vs. $I^-$) hymenium.

**TYPE:** USA, GEORGIA. Doughtery 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-
larly shaped 0.25–0.5 × 0.1–0.3 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 obvoid to obpyriform, without apical ring, 30–40 × 18–25 μm; ascospores three septate, hyaline, ±macrocephalic, becoming brownish and weakly roughened with age, I, (12.4–)12.8–18–25 lμm; (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 hodgesii 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. hodgesii 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) (fide Coppins 1989). The species also differ in their hosts, with A. graphidicola occurring on the primarily temperate species, G. scripta, and A. hodgesii 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. hodgesii 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. hodgesii to A. graphidicola.

Recently, the circumscription of the Graphidaceae has been greatly expanded to include not only the entire Thelotremataceae, 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. hodgesii. As described by Coppins (1989), A. thelotrematis differs from A. hodgesii in having reddish-brown epihymenium that is K⁺ greenish, a similarly pigmented hypothecium (vs. hyaline in A. hodgesii and A. graphidicola), as well as slightly smaller ascospores (11–14 × 4.5–5.5 μm). Based on the available literature, A. hodgesii 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 10–14 × 4–5 μm.

**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°25′01″N, 82°04′09″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; _epihyme-nium_ 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, 25–40 × 12–17 μm; _ascospores_ one septate, hyaline, ±soleiform, becoming brownish and weakly roughened with age, upper cell slightly broader and longer than lower, with an _I_+ orangish sheath, (9.4–)10.1–11.1.1–12.1(–13.7) × (3.7–)3.9–4.3–4.8(–5.6) μm (n = 52). _Pycnidia_ black, immersed in host hymenium, ca. 35–45 μm across, upper part of wall brown, lower part paler; _conidia_ hyaline, narrowly fusiform, ca. 3.7–4.5(–5.2) × 1.1–1.6(–1.8) μm.

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 eponym 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 _Artho-nia 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-
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.

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 μm in C, and 20 μm in D and E.
**Lichenochora haematommatum** 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) × (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, orbicular or irregular in shape, containing one to many perithecia, 0.2-mm across (single perithecium per gall) to 1.0-mm across (multiple perithecium 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; **paraphyses** present; hymenium filled with numerous oil droplets; **ascospores** hyaline, finally brown, occasionally weakly brown when still inside the ascus, broadly ellipsoid, one septate, constricted at the septum initially and becoming markedly so with age, (12–)12.9–14.0–15.0(–16.4) × (7.1–)7.5–8.0–8.5(–9.3) μm (n = 34), with a punctate perispore. **Pyecnidia** 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 haematommatum* 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).
Discussion. – The genus *Lichenochora* (Phyl- lachoraceae) is easily recognized by its perithe- cia, 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. haematommatum* comes closest to *L. aipoliae* Etayo, Nav.-Ros., and Coppins, a species described from Great Britain that has similar-sized, broad,
or 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) × 7–9 μm (*fide* Ihlen and Wedin 2005), they nonetheless differ from those of *L. haematommatum* 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. haematommatum* in its host, occurring on the foliose species *Physcia dubia* (Hoffm.) Lettau rather than crustose *Haematomma*.

### Additional specimens examined (all on *H. persoonii*).

- **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, ± 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 ± 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; *disces* dark blue–black, epruinose; *epihymenium* 10–20-μm thick, blue-gray pigmented, *K*; *hymenium* 50–80-μm thick, hyaline, not inspersed; *hypothecium* 25–50-μm thick, upper portions pigmented purple, *K* distinctly blue, lower portions pigmented brownish, *K* more intense brown; *exciple* bilayered, comprised of an inner layer 60–100-μm thick, comprised of *textura intricata*, lightly brownish pigmented and *K* yellow, and an outer layer 40–60-μm thick, comprised of thick, gelatinized hyphae densely inspersed with POL crystals, without pigment and *K*.


**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
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 fumarproteoctraric 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.

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 μm C–E.
(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 *M. alligatorensis* specimens of *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 (12–14 × 3.8–5.5 μm in *M. alligatorensis* vs. [13–]15–17 × 6.5–8.5 μm 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 Schum 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 (17–22 × 4–6 μm *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°56’56”N 76°24’02”W, 1 ft., swamp forest with *Chamaecyparis, Taxodium*, and mixed hardwoods (*Acer, Magnolia virginiana, Persea*) with *Lyonia-llex glabra* understory, 23 March 2013, on *Pertusaria epixantha* on large *Magnolia virginiana*, J.C. Lendemer et al. 36395 (NY!, holotype).

Description. – *Conidiomata* sporodochial-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-μm across, ca. 50-μm tall; *exciple* pigmented orange red, ±unchanged in KOH, ca. 10-μm thick, composed of relatively few ±rounded cells; *conidiophores* 7- to 14-μm long; *conidia* dark brown, obpyriform with one end truncate, 4.7–5.3–5.8 × 3.0–3.3–4.0 μm.

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 *Minutoexcipula*. Additional specimens examined. – Same locality as for the type, 23 March 2013, on *Magnolia virginiana* epixantha on large *Magnolia virginiana* under the name *M. miniatoexcipula* ’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 *Minutoexcipula*. Additional specimens examined. – Same locality as for the type, 23 March 2013, on *Magnolia virginiana* epixantha on large *Magnolia virginiana* under the name *M. miniatoexcipula* ’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 *Minutoexcipula*. Additional specimens examined. – Same locality as for the type, 23 March 2013, on *Magnolia virginiana* epixantha on large *Magnolia virginiana* under the name *M. miniatoexcipula* ’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*.
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 19. Morphology and distribution of Minutoexcipula miniatoexcipula (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. miniatoexcipula. Scale bars = 0.25 mm in A–C, 50 μm in D, and 20 μm in E.
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).
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* periphsate; *paraphyses* sparse, thin walled, unbranched, ca. 2.5- to 3.0-μm wide; *hymenial gel* I. *Asci* cylindrical, thin walled, without tholus, I', 50–65 × 11–13 μm, with 16

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.
part spores; *part spores* hyaline, tetrahedral with papillate apices, 4- to 6-µm 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* Döbbeler 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.
*Agryrium 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 anisolobum* (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 albovirescens Nyl.
Arthonia anglica Coppins
Arthonia cinnabarina (DC.) Wallr.
Arthonia hedgesii 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
+Arthroprynena cinchonae (Ach.) Müll. Arg.
+Arthroprynena taxodii R.C. Harris
Asterothyrium decipiens (Rehm) R. Sant.
Bacidia diffracta S. Ekman
Bacidia helicospora 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.) Vézda
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 eliae (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 trypetheli (Tuck.) Fink
Bulbothrix isidiza (Nyl.) Hale
Bulbothrix scortella (Nyl.) Hale
Byssoloma leucobapharum (Nyl.) Vain.
Byssoloma meadii (Tuck.) S. Ekman
Calopla caampa tidita (Tuck.) Zählbr.
Calopla caampa tidita (Tuck.) Zahlbr.
Calopla caampa tidita (With.) J.R. Laundon
Candelariella xanthostigmoids (Müll. Arg.) R.W. Rogers
Canoparmelia amazonica (Nyl.) Elix & Hale
Canoparmelia caroliniana (Nyl.) Elix & Hale
Catinaria atropurpurea (Schaer.) Vézda & Poelt
Chaeophyta hygrophila Tibell
Chaeonothecopsis debilis (Sm.) Tibell
Chaeonothecopsis nana Tibell
Chaeonothecopsis pusilla (Ach.) A.F.W. Schmidt
Chaeonothecopsis pusiola (Ach.) Vain.
Chrysothrix chamaeigracilis (Ach.) A.F.W. Schmidt
Cladonia atlantica A. Evans
Cladonia baumontii (Tuck.) Vain.
Cladonia caespiticia (Pers.) Flörke
Cladonia didyma var. vulcanica (Zoll. & Marett) Vain.
Cladonia evansii Abbayes
Cladonia incrassata Flörke
Cladonia leporina Fr.
Cladonia macilenta var. bacillaris (Genth) Schaer.
Cladonia ochrochora Flörke
Cladonia parasitica (Hoffm.) Hoffm.
Cladonia peziformis (With.) J.R. Laundon
Cladonia polycarpha 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
Coniambigua phaeographidis (Etayo & Dieudenrich)

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. leucopodium (Tuck.) Degel.
Collema subflaccidum Degel.
*Coniambigua phaeographidis Etayo & Dieudenrich
Coniarthonia pyrrhula (Nyl.) Grube
*Cornutispora triangularis* Diederich & Etayo
*Crespoa crozalsiana* (Harm.) Lendemer & B.P. Hodk.
*Crespeaflava* (Vain.) Egea &Torrente
*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.
*Dyplolabia 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.) Stagier
*Flavoparmelia caperata* (L.) Hale
*Gyalideopsis buckii* Lücking, Sérus., & Vězda

*Gyalideopsis floridae* Etayo & Diederich
*Graphis cincta* (Pers.) Aptroot
*Graphis crebra* Vain.
*Graphis desquamescens* Fée
*Graphis duplicata* Ach.
*Graphis endoxantha* Fée
*Graphis handelii* Zahlbr.
*Graphis intermedians* Vain.
*Graphis inversa* R.C. Harris
*Graphis lineola* Ach.
*Graphis pinicola* Zahlbr.
*Graphis scripta* (L.) Ach.
*Graphis striata* (Ach.) Spreng.
*Graphis tenella* Ach.
*Graphis vittata* Müll. Arg.
*Gyalideopsis buckii* Lücking, Sérus., & Vězda
*Gyalideopsis floridai* Etayo & Diederich
*Haematoma Persoonii* (Fée) A. Massal.
*Hafelia* 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 leucomeilos* (L.) Poelt
*Heterodermia obscurata* (Nyl.) Trevis.
*Hypotrachyna cryptochlora* (Vain.) D. Hawksw. & A. Cresfield
*Hypotrachyna horrescens* (Taylor) Swinsc. & Krog
*Hypotrachyna livida* (Taylor) Hale
*Hypotrachyna minarum* (Vain.) Krog & Swinsc.
*Hypotrachyna osseolba* (Vain.) Y.S. Park & Hale

*Intralichen lichenum* (Diederich) D. Hawksw. & M.S. Cole
*Lecanora caesiorubella* (Diederich) D. Hawksw.
*Lecanora chlarotera* Nyl.
*Lecanora cinereofusca* H. Magn.
*Lecanora cupressi* Tuck.
*Lecanora floridula* Lumbsch
*Lecanora hybocarpa* (Tuck.) Brodo
*Lecanora imshaugii* Brodo
*Lecanora louisianae* B. de Lesdorf
*Lecanora nothocaesiella* R.C. Harris & Lendemer
*Lecanora stroblina* (Spreng.) Kieff.
*Lecanora subpallens* Zahlbr.
*Lepraria finkii* (B. de Lesdorf) R.C. Harris
*Leptogium austroamericanum* (Malme) C.W. Dodge

*Leptogium azureum* (Sw.) Mont.
*Leptogium corticola* (Taylor) Tuck.
*Leptogium cyanescens* (Rabenh.) Körb.
*Lichenoconium cargillianum* (Linds.) D. Hawksw.
Lichenoconium 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.) Mül. 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 (Mül. Arg.) Hale

Parrotremata hypoleucinum (J. Steiner) Hale

Parrotremata hypotropum (Nyl.) Hale

Parrotremata interneum (Nyl.) Hale

Parrotremata madagascariaceum (Hue) Hale

Parrotremata mellissii (C.W. Dodge) Hale

Parrotremata neotropicum Kurok.

Parrotremata perforatum (Jacq.) A. Massal.

Parrotremata praeisorediosum (Nyl.) Hale

Parrotremata rampoddense (Nyl.) Hale

Parrotremata reticulatum (Taylor) M. Choisy

Parrotremata subsisidiosum (Müll. Arg.) Hale

Parrotremata submarginale (Michx.) DePriest & B. Hale

Parrotremata subrigidum Egan

Parrotremata tinctorum (Nyl.) Hale

Parrotremata ultralucens (Krog) Hale

Parrotremata xanthinum (Müll. Arg.) Hale

Peltigera neopolydactyla (Gyeln.) Gyeln.

Pertusaria epiantha R.C. Harris

Pertusaria neosotica I.M. Lamb

Pertusaria obruta R.C. Harris

Pertusaria paratuberculifera Dibben

Pertusaria propingua Müll. Arg.

Pertusaria pustulata (Ach.) Duby

Pertusaria sinusmexicana Dibben

Pertusaria subpertusa Brodo

Pertusaria tetrahalamia (Fée) Nyl.

Pertusaria texana Müll. Arg.

Phaeocalicium polyporaeum (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 (Sürt.) 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 scabrida R.C. Harris
*Pronectria subimperspicua (Speg.) Lowen
Protoparmelia isidiata Diederich, Aptroot & Sérus.
Pseudosagedia cestrensis (Tuck.) R.C. Harris
Pseudosagedia isidiata (R.C. Harris) R.C. Harris
Pseudosagedia rhaphidosperma (Müll. 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 citriforis R.C. Harris
Pyrenula cruenta (Mont.) Vain.
Pyrenula leucostoma Ach.
Pyrenula mamillana (Ach.) Trevis.
Pyrenula microcarpa Müll. 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.) Müll. Arg.
Pygillus javanicus Nyl.
Pyrrhospora sp. This species, widespread in the southeastern Coastal Plain, has been confused with Pyrrhospora quernea (Dicks.) Körb. 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 albovirens (G. Mey.) Aptroot
Pyxine caesiopruinosa (Nyl.) Imshaug
Pyxine sorediata (Ach.) Mont.
Pyxine subcinerea Sturt.
Ramalina complanata (Sw.) Ach.
Ramalina culbersoniourum LaGreca
Ramalina stenospora Müll. Arg.
Ramalina willeyi R. Howe
Ramboldia russula (Ach.) Kalb, Lumbsch & Elig
Ramonia microspora Vězda
Rinodina dolichospora Malme
Rinodina maculans Müll. Arg.
Rinodina papillata H. Magn.
Ropalospora viridis (Tønsberg) Tønsberg
*Roselliniopsis tropica Matzer & R. Sant.
Sarcographa tricosa (Ach.) Müll. 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 Melaspidea 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 lepta (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 (Fée) Staiger
Thalloloma hypoleptum (Nyl.) Staiger
Thelopsis rubella Nyl.
Thelotrema adjectum Nyl.
Thelotrema defectum R.C. Harris
Thelotrema dilatatum (Müll. Arg.) Hale
Thelotrema lathraeum Tuck.
Thelotrema monospermum R.C. Harris
Thelotrema subtile Tuck.
Topelia aperiens P. M. Jørg. & Vžda
Træpeliosis flexuosa (Fr.) Coppins & P. James
*Tremella parmelia R.C. Harris
*Tremella harrii R.C. Harris
*Tremella pertusaria R.C. Harris
*Tremella phaeographidis R.C. Harris
*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.) Müll. Arg.
Trypethelium virescens Tuck.
Tuckermanella fendleri (Nyl.) Essl.
Usnea baileyi (Stirt.) Zahlbr.
Usnea endochrysea Sturt.
Usnea evansii Motyka
Usnea mutabilis Sturt.

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Usnea pensylvanica Motyka
Usnea strigosa (Ach.) Eaton
Usnea subscabrosa Motyka
Usnea trichodea Ach.
Variolaria amara Ach.
Variolaria commutata (Mull. Arg.) ined. (≡Pertusria commutata Mull. Arg.)
Variolaria hypothamnolica (Dibben) ined. (≡Pertusria hypothamnolica Dibben)

Variolaria multipunctoides (Dibben) Lendemer, B.P. Hodk., & R.C. Harris
Variolaria ophthalmizia (Nyl.) Darb.
Variolaria pustulata (Brodo & W.L. Cubl.) 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
2. 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
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 fruticoso or large squamulose ......................................................... 7
6. 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 fruticoso; not Cladonia/ Cladina
   Key 6. Fruticoso Macrolichens
4. Thallus crustose ..................................................................................... 8
8. Thallus on leaves ............................................. Key 7. Foliicolous 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
11. Ascospores colorless .............................................................................. 11
   Key 10. Crustose Apotheciate Lichens with Hyaline Spores
11. Ascospores brown .................................................................................. 12
   Key 11. Crustose Apotheciate Lichens with Brown Spores
KEY 1. LICHENICOLOUS FUNGI

1. Spores produced in ascii in disciform, lirelliform or flask shaped structures .................................................. 2
2. Ascomata disk-like (apothecioid) or lirelliform (if hemispherical apothecioid but without asci, see
\textit{Tremella}) ................................................................. 3
3. Spores soon brown, simple or 1-septate ............................................................... 4
4. Ascomata with short stalk; spores simple, citriform (lemon-shaped), coarsely ridged ......................... \textit{Sphinctrina tubiformis} A. Massal
4. Ascomata not stalked; spores 1-septate ................................................................. 5
5. Ascomata lirelliform; on \textit{Pyrenula cruenta} .......................................................... 5

6. On thallus of \textit{Parmotrema subrigidum}; epihymenium K+ green .......................... 6
6. On thallus of \textit{Parmotrema subrigidum}; epihymenium \textit{KOH+} green................. \textit{Abrothallus parmotrematis} Diederich
7. On \textit{Bathelium carolinianum}; spores 16–19 × 8–11.5 μm ........................................... \textit{Buellia trypethelii} (Tuck.) Fink
7. On \textit{Pertusaria} ...................................................................................................................... 8
8. Asci with I+ blue cap; spores 12–15 × 6–8.5 μm; on \textit{Pertusaria parutuberculifera} ............. \textit{Dactylospora inquilina} (Tuck.) Hafellner
8. Asci without I+ cap; spores 15–18 × 6–8 μm on \textit{Pertusaria tetratalamia} ................. \textit{Buellia minimula} (Tuck.) Fink
9. Ascomata dark, \textit{K}+/\textit{Ca}− .......................................................................................... 9
10. Spores simple ................................................................................................................. 10
11. On thallus of \textit{Lecanora floridula} and \textit{L. louisianae}; ascomata with marginal hairs; asci 8-spored, ellipsoid, 7–9 × 3–3.5 μm . . . \textit{Skytnea lecanorea Diederich & Etayo}
11. On thallus of \textit{Parmotrema submarginale} & \textit{P. subrigidum}; ascomata without marginal hairs; asci multisporous; spores ± globose to broadly ellipsoid . . . \textit{Gyalideopsis floridiae} Etayo & Diederich
12. Spores 1-3-septate ........................................................................................................... 12
13. Ascomata not stalked, not mazaedial; on \textit{Haematomma accolens} or \textit{Pyrenula cruenta} ................................................................. 14
14. Growing in hymenium of \textit{Haematomma accolens}; ascomata blotchy, irregularly shaped ... \textit{Arthonia stevensoniana} R.C. Harris & Lendemer
15. On thallus of \textit{Lecanora louisianae}; spores 2(–3)-septate, 13–16 × 5–7.5 μm ...........
16. \textit{Arthonia agelastica} R.C. Harris & Lendemer
17. Spores brown ................................................................................................................. 17
18. Asci multisporous; spores 1-septate; on various crustose lichens (incl. \textit{Buellia curtisi},
\textit{Lecanora strobilina}, \textit{Pertusaria epixantha} and \textit{P. obruta}) ................................................................. \textit{Arthonia hodgesii} Lendemer & R.C. Harris
18. Asci 8-spored ................................................................................................................ 18
19. Ascospores simple; on apothecia and thallus of \textit{Ochrolechia africana} ......................... \textit{Muellerella lichenicola} (Sommerf.) D. Hawksw.
20. Spores 1-3-septate ........................................................................................................ 16
21. Apothecia orange, K+ purple or whitish to pinkish ..................................................... 16
22. Apothecia orange, K+ red; spores 3-septate, macrocephalic, 12–15 × 4–7 μm; on \textit{Graphis
lineata} ................................................................................ \textit{Arthonia hodgesii} Lendemer & R.C. Harris
23. Apothecia whitish to pinkish; margin concolorous or paler than disk; epihymenium and exciple filled with small \textit{POL+} crystals; spores needle shaped; over thallus of \textit{Trypethelium tropicum} ......................... \textit{Bacidia crystallicifera} Ekman
24. Spores 2-3-septate ...................................................................................................... 15
25. On thallus of \textit{Lecanora louisianae}; spores 2(–3)-septate, 13–16 × 5–7.5 μm ...........
26. \textit{Arthonia agelastica} R.C. Harris & Lendemer
27. On \textit{Pertusaria}; spores 3-septate, 17–26 × 6.5–9 μm .................................................. \textit{Opegrapha anomaea} Nyl.
28. Ascomata orange, KOH+ purple or whitish to pinkish ................................................ 16
29. Apothecia orange, K+ red; spores 3-septate, macrocephalic, 12–15 × 4–7 μm; on \textit{Graphis
lineata} ................................................................................ \textit{Arthonia hodgesii} Lendemer & R.C. Harris
30. Apothecia whitish to pinkish; margin concolorous or paler than disk; epihymenium and exciple filled with small \textit{POL+} crystals; spores needle shaped; over thallus of \textit{Trypethelium tropicum} ......................... \textit{Bacidia crystallicifera} Ekman
31. Ascomata with short stalk, mazaedial; on apothecia and thallus of \textit{Lecanora
caesiorubella} ssp. \textit{glaucomodes}, \textit{L. louisianae} and \textit{L. subpallens} ................................ [\textit{Chaenothecopsis kalbii} Tibell & K. Ryman]
32. Spores 2-3-septate ...................................................................................................... 15
33. On thallus of \textit{Lecanora louisianae}; spores 2(–3)-septate, 13–16 × 5–7.5 μm ...........
34. \textit{Arthonia agelastica} R.C. Harris & Lendemer
35. On \textit{Pertusaria}; spores 3-septate, 17–26 × 6.5–9 μm .................................................. \textit{Opegrapha anomaea} Nyl.
36. Ascomata with short stalk, mazaedial; on apothecia and thallus of \textit{Lecanora
caesiorubella} ssp. \textit{glaucomodes}, \textit{L. louisianae} and \textit{L. subpallens} ................................ [\textit{Chaenothecopsis kalbii} Tibell & K. Ryman]
1. Spores not produced in asci, but rather in flask-shaped or disciform structures (pycnidia, sporodochia), tiny
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24. Spores produced in pycnidia, sporodochia, or tiny stromata ............................................... 2 5
(''hyphomycetes'')................................................................................................. 2 4
Phaeosporobolus

25. Spores brown or greenish ............................................................................. 2 6
25. Spores colorless ....................................................................................... 3 5

17. Spores colorless or pale brownish (may turn dark brown in age), 1-septate . . . ...................... 2 0

26. Conidioma a pycnidium .......................................................................... 2 7
3
35. Conidia broadly ellipsoid, 3.5–6 × 3–4 μm, with a single guttule; on Parmeliaceae, esp.
Punctelia rudenta .......................................................... Didymocyrtis melanelixiae (Brackel) Diederich,
R.C. Harris & Etayo (Phoma asexual stage)
35. Conidia tetrahedral (triangular in surface view); apices papillate on Pertusaria subpertusa
.................................................. Cornutispora triangularis Diederich & Etayo

30. Conidia pyriform, 8–10 μm; on Pertusaria.......................................................... Minutoexcipula mariana V. Atienza
30. Conidia globose, 5–6 μm; on Lecanora hybocarpa ........................................... Lichenonomium carginallinum (Linds.) D. Hawksw.

22. Perithecia pink, fuzzy; spores of two sizes ........................................... [Oviculospora parmeliae (Berk. & M. A. Curtis) Etayo]
22. Perithecia reddish with short colorless setae; spores all one size; on various
crustose lichens (incl. Micarea prasina) .................................................. Nectriopsis rubeacens (Ellis & Everh.) M.S. Cole & D. Hawksw.

20. Perithecia black .................................................................................. 2 3
20. Perithecia pink, orangish or reddish ............................................................. 2 1
20. Perithecia immersed in thallus of Punctelia rudenta; wall orangish, K+ purplish spores
uniseriate, 8–10 × 5–6 μm, warty ........... Pronectria subimpressipaecua (Spec.) Lowen

19. Ascospores submuriform; on Rinodina maculans ................................. Merismatium sp.
17. Spores colorless or pale brownish (may turn dark brown in age), 1-septate .......................... 2 0
20. Perithecia pink, orangish or reddish ............................................................. 2 1
21. Perithecia immersed in thallus of Punctelia rudenta; wall orangish, K+ purplish spores
uniseriate, 8–10 × 5–6 μm, warty ........... Pronectria subimpressipaecua (Spec.) Lowen
21. Perithecia superficial; pink or reddish; wall K– ........................................... 2 2
18. Perithecia on crustose lichens, wall K– ..................................................... 2 3
22. Perithecia pink, fuzzy; spores of two sizes ........................................... [Oviculospora parmeliae (Berk. & M. A. Curtis) Etayo]
22. Perithecia reddish with short colorless setae; spores all one size; on various
crustose lichens (incl. Micarea prasina) .................................................. Nectriopsis rubeacens (Ellis & Everh.) M.S. Cole & D. Hawksw.

23. Asci 16-spored (part spores); part spores tetrahedral; perithecia with setae around
ostiole; in thallus of Punctelia rudenta.......................................................... Trichosphaerella buckii R.C. Harris & Lendemer

23. Asci 16-spored (part spores); part spores tetrahedral; perithecia with setae around
ostiole; in thallus of Punctelia rudenta.......................................................... Trichosphaerella buckii R.C. Harris & Lendemer
24. Spores produced by hyphae embedded in apothecia or thallus (“hyphomycetes”) or basidiomata (not in pycnidia or sporocidia) .......................................................... 36

36. Hyphomycetes ............................................. 37

37. Conidia (1–2)-septate, 7–11 × 3.5–6 μm; on Lecanora louisianae and L. subpallens ..............

Intransilichen lichenum (Diederich) D. Hawksw. & M.S. Cole

36. Basidiomycetes ............................................. 38

38. On Parmotrema perforatum ......................... Tremella parmetarium Diederich
38. On Pertussaria ............................................. Tremella pertusariae Diederich
38. On Leiorreuma ......................... Tremella phaeographidis Diederich, Coppins & Bandoni
38. On Bathelium carolinianum ......................... Tremella harrisii Diederich
38. On Lecanora louisianae ..................................... Tremella sp.

KEY 2. CALICIOID FUNGI

1. Ascospores simple ........................................ 2
2. Ascospores ellipsoid; thallus not evident; on bark and wood ....... Mycocalicum subtile (Pers.) Szatala
2. Ascospores globose, simple; thallus granulose, green; on Chamaecyparis and Taxodium.......... Chaenotheca hygrophila Tibell

1. Ascospores 2-celled ...................................... 3
3. On the polypore Trichaptum biforme ........... Phaeocalicium polyproareum (Nyl.) Tibell
3. On wood ..................................................... 4
4. Capitulum K- or K+ intensifying, but not K+ red ................................................................. 5
5. Ascospores with septum distinctly more lightly pigmented than the walls......................... Chaenothecopsis pusiola (Ach.) A.F.W. Schmidt
5. Ascospores with normally pigmented septum just as dark as the walls ......................... 6
6. Stalks tall, reddish pigmented, C+ fleeting greenish in section ........................................ Chaenothecopsis debilis (Sm.) Tibell
6. Stalks short, not reddish pigmented, C- ................................ Chaenothecopsis nana Tibell

KEY 3. FOLIOSE CYANOLICHENS

1. Thallus isidiate or lobulate, with lichenized diaspores; apothecia rarely produced ...................... 2
2. Medulla P-, isidiate or lobulate .......................................................... 3
3. Thallus slate or lead gray .................................. 4
4. Thallus thick, with a conspicuous weft of rhizines not gelatinous when wet ......................... 5
5. Thallus isidiate; common ...... Coccocarpia palmicola (Spreng.) Arv. & D.J. Galloway
5. Thallus lobulate; rare ....................................... Parmeliella pannosa (Sw.) Müll. Arg.
4. Thallus thin, without rhizines, gelatinous when wet .......................................................... 6
6. Thallus smooth, isidia or lobules distributed more-or-less evenly across the surface ...........
Leptogium cyanescens (Rabenh.) Körb.
6. Thallus wrinkles, isidia or lobules often somewhat concentrated on the wrinkled ..........
Leptogium austroamericanum (Malme) C.W. Dodge
3. Thallus black or brown ..................................... 7
7. Thallus black; isidia globose ................................ Collea subfuscacidum Degel.
7. Thallus brown; isidiate or lobulate .......................................................... 8
8. Thallus fruticos, a complex tangle of intensely divided minute lobes, resembling
Leptogium lichenoides .................................. Dendrisiscoconcal intricatum (Nyl.) Henssen
8. Thallus foliose, with distinct plane lobes bearing marginal phyllidia ....................................... 9
9. Medulla white, K- ....................................... Sticta carolinensis T. McDonald
9. Medulla orange, K+ purple ................................ Sticta deyana Lendemer & Goffinet
1. Thallus without lichenized diaspores; apothecia frequently produced ................................. 10
10. Thallus growing on the ground or over organic matter at the bases of trees; lower surface with a distinct network of veins and long rhizines ........................................ Peltigera neopolydactyla (Gyeln.) Gyeln.
KEY 4. FOLIOSE CHLOROLICHENS

1. Thallus not pustulose, sorediate, isidiate, or phyllidiate; apothecia densely white pruinose
   ......................................................... 2

2. Thallus with a distinct black, felt-like hypothallus on the lower surface; very rare
   ......................................................... 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
   ......................................................... 5

5. Apothecia entire, not perforated with a hole in the center; medulla P
   ......................................................... 6

6. Medulla UV- (alectoronic acid absent); typically inland
   ......................................................... 7

7. Medulla, especially near the apothecia, K- (norstictic acid absent) ........................................ 8

8. Thallus gray to greenish; with pale rhizines if rhizines are present; main photobiont a green alga
   ......................................................... 9

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
    ......................................................... 11

11. Upper cortex and medulla K+ yellow (atranorin present); lobes not abundantly lobulate
    ......................................................... 12

12. Thallus truly foliose, with distinct marginal lobes
    ......................................................... 13

13. Lobes lead gray; with a distinct weft of dark rhizines; main photobiont a cyanobacterium
    ......................................................... 14

14. Lower surface with abundant rhizines
    ......................................................... 15

15. Thallus wrinkled
    ......................................................... 16

16. Thallus dark greenish-brown to brown, forming minute rosettes on conifer branches
    ......................................................... 17

17. Thallus gelatinous (jelly-like) when wet
    ......................................................... 18

18. Thallus lead gray; with a distinct weft of dark rhizines; main photobiont a green alga
    ......................................................... 19

19. Thallus not pustulose, sorediate, isidiate, or phyllidiate; apothecia uncomonic
    ......................................................... 20

Collema pulcellum (Tuck.) Degel.

Fuscopannaria leucosticta (Tuck.) P. M. Jørg.

Lobaria ravenelii

Parmotrema submarginale (Michx.) DePriest & B. Hale

Parmotrema perforatum (Jacq.) A. Massal.

Parmotrema subrigidum

Parmotrema submarginale Egan s. str.

Parmotrema subrigidum Egan s. lat.

Tuckermanella fendleri (Nyl.) Essl.

Leptogium azureum

Leptogium corticola

Pannaria lurida

Ruprechtia livida

Tuckermanella fendleri (Nyl.) Essl.

Parmotrema perforatum (Jacq.) A. Massal.

Parmotrema submarginale (Michx.) DePriest & B. Hale

Parmotrema subrigidum

Parmotrema submarginale Egan s. str.

Parmotrema subrigidum Egan s. lat.

Tuckermanella fendleri (Nyl.) Essl.

Parmotrema perforatum (Jacq.) A. Massal.

Parmotrema submarginale (Michx.) DePriest & B. Hale

Parmotrema subrigidum

Parmotrema submarginale Egan s. str.

Parmotrema subrigidum Egan s. lat.

Tuckermanella fendleri (Nyl.) Essl.

Parmotrema perforatum (Jacq.) A. Massal.

Parmotrema submarginale (Michx.) DePriest & B. Hale

Parmotrema subrigidum

Parmotrema submarginale Egan s. str.

Parmotrema subrigidum Egan s. lat.

Tuckermanella fendleri (Nyl.) Essl.
12. Thallus with a distinct black, felt-like hypothallus on the lower surface; lobe margins abundantly isidiate/phyllidiate .................................................................................. \textit{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 isidiate .................................................................................. 16

15. Lower surface black, at least centrally; lobules fine, erect, fragile.......................................................... \textit{Phaeophyscia squarrosa} Kashiw.

15. Lower surface pale to tan throughout; lobules coarse and robust, not erect, not fragile .......................... \textit{Anaptychia palmulata} (Michx.) Vain.

14. Thallus isidiate .................................................................................. 16

16. Lower surface ecorticate, orange pigmented; orange pigment K$^+$ purple .................................................. \textit{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 present .......................................................... 20

20. Thallus isidiate; isidia short to tall, cylindrical, brown tipped, not clustered only in the pseudocyphellae.......................................................... \textit{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 .......................................................... \textit{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) ............ \textit{Parmotrema madagascariaceum} (Hue) Hale

21. Upper surface blue-gray, K$^+$ yellow, KC$^-$ (atranorin present) ................................ \textit{Parmotrema tinctorum} (Nyl.) Hale

18. Lobes narrow, <3 mm wide .................................................................................. 22

22. Marginal cilia with bulbate bases; lower surface brown .............................................................................. \textit{Bulbothrix scortella} (Nyl.) Hale

22. Marginal cilia without bulbate bases; lower surface black .............................................................................. \textit{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 ........................................ \textit{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 .......................................................... \textit{Parmotrema internexum} (Nyl.) Hale

26. Medulla P$^+$ red (protocetraric acid present); upper surface with white pseudocyphellae. .......................................................... \textit{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) ................................ \textit{Parmotrema ultralucens} (Krog) Hale

27. Entire medulla UV$^-$ .................................................................................. 28

28. Lower surface black .................................................................................. \textit{Parmotrema subisidiosum} (Müll. Arg.) Hale

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 ...................... Parmotrema mellissii (C.W. Dodge) Hale
31. Medulla UV+ blue-white (alectoronic acid present); upper cortex blue-gray, K+ yellow, KC- (atranorin 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 osseoalba (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 rubropalchra (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

46. Upper surface yellow or yellow green (calycin or usnic acid present)  

47. Soralia marginal/terminal, not laminal; upper surface yellow, KC- (calycin present)  

48. Lobes broad, >3 mm wide; medulla P+ orange-red, UV- (proto-cetraric acid present)  

49. Upper cortex gray-brown, K- (atranorin absent); capitate soralia terminal on the tips of secondary lobes  

50. Medulla C+ pink-red (gyrophoric or lecanoric acid present)  

51. Lower surface pale; upper surface with conspicuous white pseudocyphellae; squamiform soredio-idiada present and clustered in the pseudocyphellae  

52. Thallus with coarse pustules; common  

53. Medulla K- or K+ yellow-brown, but not K+ yellow turning red  

54. Lobes narrow, <1 mm wide; medulla P-, UV+ blue-white (divaricatic acid present)  

55. Lobes strongly ascending; lower surface with broad white blotches especially near the margins  

56. Medulla K+ yellow turning red, producing norstictic acid crystals, P+ yellow (norstictic acid present)  

57. Diffuse soralia with coarse soredia present on the tips of the sublobes  

58. Medulla K- or K+ yellow-brown, but not K+ yellow turning red
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] ...........................................

58. Medulla P- (protocetraric acid or stictic acid absent) . . . 61
62. Lobes broad, >3 mm wide ...................................... 63
63. Medulla UV- (fatty acids present) ...........
63. Medulla UV+ blue-white (alectoronic acid present) .................... Parmotrema praesorediosum (Nyl.) Hale
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 sorediosa (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/ymenia red; primary squamules conspicuously sorediate; thallus P+ ......... .......................... Cladonia incrasata Flörke

7. Apothecia/ymenia brown; primary squamules esorediate; thallus P+ or red ........................................... 8

8. Podetia tall, little branching, forming funnels; thallus UV+ yellow, orange or red ................................................................. 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 peziformis (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 polycairia G. Merr.

5. Podetia with a discontinuous cortex, with some parts dissolving into soredia or microsquamules . 10

10. Apothecia/ymenia red ................................................................................ 11

11. Podetia sorediate, with the soredia abrading to reveal remnants of the loose medulla or the opaque white stereome; thallus P+ (barbic acid present) ............................................................. Cladonia macilenta var. bacillaris (Genth) Schae.

11. Podetia microsquamulose, with the microsquamules sloughing off to reveal the naked translucent stereome; thallus P+ (barbic acid present) or P+ orange (thamnolic acid present) ................................................................. 12

12. Thallus P+ orange (thamnolic acid present) ............................................. Cladonia didyma var. vulcanica (Zoll. & Moritzi) Vain.

12. Thallus P- (barbic acid present). .... Cladonia didyma var. didyma (Fée) Vain.

10. Apothecia/ymenia brown ........................................................................ 13

13. Thallus UV+ blue-white and P+ yellow (squamatic acid and baemycetic acid present) .................................................. Cladonia canumontii (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 ........................................... Cladonia subradiata (Vain.) Sandst.

1. Podetia absent; thallus entirely composed of primary squamules ................................. Cladonia caespiticia (Pers.) Flörke

18. Conspicuous apothecia present, borne directly on a short stipe arising from the primary squamules . 18

18. Apothecia absent .................................................................................. Cladonia caespiticia (Pers.) Flörke

19. Thallus P+; ymicia 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; barbic acid present ...... Cladonia macilenta var. bacillaris (Genth) Schae.
1. Thallus P+ yellow, orange or red; pycnidia brown or red .............................................. 21
2. 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 baumontii (Tuck.) Vain.
21. Thallus P+ 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 “sidioid” microsquamules; 
 pycnidia brown .................................................. Cladonia parasitica (Hoffm.) Hoffm.
25. Primary squamules typically remaining intact, sometimes dissolving into 
soredia; pycnidia red .............................................. 26
 ................................................................. Cladonia didyma var. vulcanica (Zoll. & Moritzi) Vain.
23. Thallus K- or K+ dingy yellow-brown ................................................................. 27
26. Thallus P+ orange (stictic acid present); squamules erect, not dissolving ...........
 ................................................................. Cladonia polycarpa G. Merr.
26. Thallus P+ red (fumarprotocetraric acid present); squamules plane or decumbent, 
dissolving or not .................................................. 28
27. Primary squamules dissolving entirely into soredia ............................................. 29
 ................................................................. Cladonia ramulosa (With.) J.R. Laundon
27. Primary squamules remaining intact, at least for the most part ..................... 30
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 ochrochlorea 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 homosekikaïc 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 proporocetraric acid 
 present ........................................................... Ramalina villegyi 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) .................................. 9
8. Medulla without lichen substances (TLC required) ......................................... 10
 ................................................................. [Ramalina americana Hale, present just north of DRBH]
3. Branches with a central cord or cavity ............................................................. 11
9. Thallus without soredia or isidia; apothecia typically present .......................... 12
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 ................................ 13

19. Thallus P+ yellow, orange or red; pycnidia brown or red ................................. 21
20. Thallus P+ yellow (baeomycesic acid present) .................................................. 22
21. Thallus P+ red (fumarprotocetraric acid, stictic acid, or thamnolic acid present) ... 23
22. On sandy soil in disturbed areas ................................. Cladonia atlantica A. Evans
22. On bark or rotting wood in swamps ................ Cladonia baumontii (Tuck.) Vain.
21. Thallus P+ 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 “sidioid” microsquamules; 
 pycnidia brown .................................................. Cladonia parasitica (Hoffm.) Hoffm.
25. Primary squamules typically remaining intact, sometimes dissolving into 
soredia; pycnidia red .............................................. 26
 ................................................................. Cladonia didyma var. vulcanica (Zoll. & Moritzi) Vain.
1. Thallus without specialized structures for the dispersal of non-lichenized diaspores; lichenized diaspores
   present ............................................................................................................. 12
2. Nonstictic acid present ................................................................. Usnea endochrysea Stirt. s. str.
3. Nonstictic acid absent ................................................................................. 14
   4. Thallus with pale stalked pycnidia; conidia simple, ellipsoid .......................... 5
   5. Thallus with pale synnemata (stalked sporodochia); conidia compound aggregations of round cells 20
   6. Medulla P- (fat acids present); common ..................................................... 18
   7. Branches with a central cavity; medulla P+ yellow (nonstictic acid present); rare …
   8. Usnea baileyi (Stirt.) Zahlbr. ....................................................................... 17
   9. Cortex red pigmented, pigment often mottled .......................... Usnea pensylvanica Motyka
   10. Cortex not red pigmented ............................................................. 20
   11. Ascospores averaging <9 μm long; medulla pink-red pigmented; nonstictic acid absent or
       absent ............................................................................................................. 12
   12. Nonstictic acid present ................................................................. Usnea endochrysea Stirt. s. str.
   13. Nonstictic acid absent ................................................................................. 14
   14. Psoromic acid present ................................................................. Usnea strigosa (Ach.) Eaton s. str.
   15. Thamnolic acid present ................................................................. Usnea strigosa (Ach.) Eaton s. lat.
   16. Medulla pink-red pigmented .......................................................... 17
   17. Branches with a central cord; medulla P- (fatty acids present); common ........
   18. Usnea mutabilis Stirt. ............................................................................. 16
   19. Cortex long, pendant; branches with white rings (annular pseudocyphellae)........ 18
   20. Medulla P+ orange-red (protocetraric acid present) .................................... 5
   21. Medulla short, shrubby; branches without white rings .............................. 19
   22. Cortex red pigmented, pigment often mottled .......................... Usnea pensylvanica Motyka
   23. Cortex not red pigmented ............................................................. 20
   24. Medulla P- (protocetraric acid absent) ........................................ Usnea subscabrosa Motyka s. str.
   25. Medulla P- (protocetraric acid absent) ........................................ Usnea subscabrosa Motyka s. lat.

**KEY 7. FOLIOCOLOUS 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. ?

2. On leaves of *Sabal minor* or *Ilex*; thallus areolate or not, with either pale tan pycnidia or tall black sterile setae .......................... 2
   3. Thallus with hyphophores (darkened structures that resemble apically widened hairs) ......................................................... 3
   4. Thallus with pale stalked pycnidia (stalked sporodochia) .......................... 4
   5. Thallus areolate or not, with either pale tan pycnidia or tall black sterile setae . 2
   6. Photobiont Trentepohlia ............................................................................. 7

**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 ................
   4. Thallus with pale stalked pycnidia (stalked sporodochia); conidia compound aggregations of round cells .......................... **Gyalideopsis buckii** Lücking et al.
   5. Thallus with pale stalked pycnidia; conidia simple, ellipsoid ..........................
   6. Thallus UV- and P- (lobaric acid present), often P+ orange-red (fumarprotocetraric acid present) ................................................................. **Micarea neostipitata** Coppins & P. May
   7. Thallus without specialized structures for the dispersal of non-lichenized diaspores; lichenized diaspores present ................................................................. 6
   8. Photobiont Trentepohlia ............................................................................. 7

---

*Note: The text contains a table and is partially obscured in the image.*
7. Thallus sorediate .......................................................... 8

8. Soralia irregular in shape, diffuse; soredia light yellow-brown; thallus P-, typically indistinct and immersed in the substrate ................. **Opegrapha corticola** 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 ............. **Nadvornikia sorediata** R.C. Harris

7. Thallus isidiate .......................................................... 9

9. Thallus dark brown to gray .................. **Pseudosagedia isidiata** (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 ...................... **Trichothelium americanum** Lendemer

10. Thallus roughened and dull; isidia typically tall, often coraloid, conspicuous; perithecia often present, concolorous with the thallus, smooth or covered with short isidia, but never with black setae .................. **Porina scabrida** R.C. Harris

6. Photobiont coccoid .......................................................... 11

11. Thallus yellow or orange .......................................................... 12

12. On rock (concrete); thallus orange, K+ purple ........ **Caloplaca flavocitrina** (Nyl.) H. Olivier

12. On bark or wood; thallus yellow, K- .......................................................... 13

13. Thallus C- or KC+ yellow-orange (xanthones present) .................................................. 14

14. Thallus composed of flat green areoles with small, discrete, often marginal soralia; soredia yellow; typically on hardwoods ............... **Buellia wheeleri** R.C. Harris

14. Thallus composed of orange-yellow granules (leprose); soralia or soredia absent; typically on conifers .......................................................... **Pyrrhospora** sp. nov.

13. Thallus C- and KC- (xanthones absent) .......................................................... 15

15. Thallus areolate, with the areoles dissolving into piles of soredia; 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 ............... **Chrysothrix chamaeyparicola** Lendemer

16. Granules larger (>25–45 μm in diameter); thallus thicker, intense bright yellow in color (pinastic acid present); on conifers and hardwoods, often in upland habitats .................. **Chrysothrix xanthina** (Vain.) Kalb

11. Thallus green, gray, or brown .......................................................... 17

17. Thallus C+ pink (gyrophoric or lecanoric acid present; always confirmed in squash mount if C- under the dissecting microscope) .......................................................... 18

18. Thallus isidiate .................. **Placynthiella icmolea** (Ach.) Coppins & P. James

18. Thallus sorediata .......................................................... 19

19. Thallus lead gray, with dark blue-gray soredia .......................................................... 20

19. Thallus not lead gray, soredia various colors .......................................................... 20

20. Thallus light gray, continuous; "soralia" regular and discoid; on hardwoods ............. **Varicellaria velata** (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 *Pinus* .... **Placynthiella dasae** (Stirt.) Tønsberg

17. Thallus C- (gyrophoric or lecanoric acid absent) .......................................................... 21

21. Thallus UV+ bright yellow (lichexanthone present) .......................................................... 22

22. Thallus coarsely pruinosate; medulla of pustules K- (zeorin present) .................. **Megalospora pachycheila** (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) ............... **Variolaria hypothamnolica** (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 .................................................. **Variolaria commutata** (Mull. 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. Decarboxysquamatic acid present (TLC needed). ........................................

.......................... Lecanora strobilina (Spreng.) Kieff.
28. Decarboxysquamatic acid absent (TLC needed). ........................................

.......................... Lecanora cf. strobilina (Spreng.) Kieff.
25. Thallus K- or K⁺ yellow, always KC- (usnic acid or xanthones 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.)

.......................... Variolaria multipunctoides (Dibben) 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.
39. Thallus P- (above substances absent; note that occasionally atranorin gives a P⁺ yellow reaction when in high concentration) ........................................
38. Thallus UV+ blue-white (2-0-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); 2-0-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; 2-0-methylperlatolic acid present; common ........ Loxospora confusa Lendemer
43. Thallus UV- .............................................................. 43
44. Thallus sorediate or leprose (composed of granules) .............. 44
44. Thallus scruffy and dirty green in appearance, composed of gonioysts; photobiont micareoid, cells <7 μm in diameter ... 45
45. Micareic acid present (TLC required!) ......................... Micarea prasina Fr.
45. Methoxymicareic acid present (TLC required!) ........ Micarea 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, soraliate ...................... 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
49. Zeorin absent (TLC required!) .............................. Haematomma guyanense Staiger & Kalb
50. Thallus superficial, with coarse pustular soralia .......... sorediate morph of Brigantiaea leucoxantha
50. Thallus superficial, with coarse pustular soralia .......... Lecanora nothocaesiella R.C. Harris & Lendemer
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 oligotropha* (J.R. Laundon) Coppins & P. James]

55. Thallus more-or-less a continuous film of minute dark-brown to blackish areoles ...... [*Placynthiella uliginosa* (Schrad.) 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.) M üll. 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.) M üll. Arg.]

KEY 9. CRUSTOSE PYRENOLICHENS

1. Ascospores hyaline ................................................................................................. 2
2. Ascospores submuriform or muriform ................................................................. 3
3. Perithecia pale white; thallus scurfy, greenish, composed of goniocysts................

............................................................................ *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. & V ézda
4. Perithecia black, conspicuous; ostiole lateral; ascospores 40–55 × 15–20 μm; thallus gray to white, ecorricate, 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; pseudostroma brown and with yellow pigmented tissue in the space between the perithecia …………………………… Bethelium 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 20–27 × 6.5–8 μm …………………………… 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 pseudostromata ………………… 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 μm long ………………………………………………… 16

16. Ascospores narrow, 3–5 μm wide, filiform; perithecial wall dark purple-black in section …………………………… Pseudosagedia rhaphidosperma (Müll. Arg.) R.C. Harris

16. Ascospores broad, 10–15 μm wide, clavate; perithecial wall brown to orange in section ……………………… Porina heterospora (Fink) R.C. Harris

15. Ascospores <70 μm 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 × 2–3 μm; parasitic on algal colonies; rarely collected …………………………… Epigloea pleiospora Döbbeler

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 × 5–7 μm …………………………… Mycoporum eschweileri (Müll. Arg.) R.C. Harris

20. Ascospores 20–27 × 6.5–8 μm …………………………… 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 10–18 × 4–7 μm ………………………………………………… 24

24. Ascospores distinctly biseriate or irregularly arranged, with a submedian or median septum ………………… 25

25. On hardwoods; ascomata superficial ………………………………………………… 26

21. Ascospores <20 μm long; photobiont distinctly visible …………………………… 26

24. On Taxodium; ascomata immersed …………………………… Arthopyrenia taxodii R.C. Harris

25. On Taxodium; ascomata immersed …………………………… Arthopyrenia taxodii R.C. Harris
<table>
<thead>
<tr>
<th>Step</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Ascospores brown .................................................................</td>
</tr>
<tr>
<td>29.</td>
<td>Ascospores muriform ...............................................................</td>
</tr>
<tr>
<td>30.</td>
<td>Ascospores 130–225 × 38–50 μm long, 2 per ascus ..........................</td>
</tr>
<tr>
<td>31.</td>
<td>Ascospores small, 30–42–[53] × 11–15 μm; known from nearby Great Dismal Swamp.</td>
</tr>
<tr>
<td>32.</td>
<td>Thallus corticate, brown or greenish brown; perithecia not as above ..............................</td>
</tr>
<tr>
<td>33.</td>
<td>Thallus corticate, brown or greenish brown; perithecia not as above ..............................</td>
</tr>
<tr>
<td>34.</td>
<td>Ascospores 130–225 × 38–50 μm long ........................................</td>
</tr>
<tr>
<td>35.</td>
<td>Ascospores &lt;70 μm long, 8 per ascus ...........................................</td>
</tr>
<tr>
<td>36.</td>
<td>Ascospores larger, 45–70 × 16–30 μm ...........................................</td>
</tr>
<tr>
<td>39.</td>
<td>Ostiole apical; thallus thin or thick .........................................</td>
</tr>
<tr>
<td>40.</td>
<td>Ostiole apical; thallus thin or thick .........................................</td>
</tr>
<tr>
<td>37.</td>
<td>Thallus UV+ yellow (lichexanthone present); often on bases and boles of trees.</td>
</tr>
<tr>
<td>38.</td>
<td>Thallus UV- (lichexanthone absent); often on the stems of shrubs.</td>
</tr>
<tr>
<td>39.</td>
<td>Thallus corticate, brown or greenish brown; perithecia not as above ..............................</td>
</tr>
<tr>
<td>40.</td>
<td>Ascospores &gt;25 μm long ................................................................</td>
</tr>
<tr>
<td>41.</td>
<td>Hymenium densely inspersed with oil droplets. ............................</td>
</tr>
<tr>
<td>41.</td>
<td>Hymenium not inspersed .........................................................</td>
</tr>
</tbody>
</table>

**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 ...................................... 2
4. Thalloloma cf. cinnabarina (Fée) Staiger [collections often without ascospores]
5. Pigment red or orange, K+ purple .............................................. 67
4. Apothecia black, narrowly elongate and lirelliform; exciple carbonized laterally; orange pigment in the epihymenium, pigment K+ purple .................. Graphis inversa R.C. Harris

5. Apothecia irregular in shape, with a distinct margin and disc; ascospores clavate, 4-celled, macrocephalic .................................. Arthonia cinnabarina (DC.) Wallr.

6. Ascospores present ......................... Coniarthonia pyrrhula (Nyl.) Grube

7. Apothecia red, irregularly shaped but not narrowly elongate and lirelliform .................... 5

8. Ascospores transversely sejate; photobiont coccoid .............................. Arthonia albovirescens Nyl.

9. Ascospores submuriform to muriform; photobiont Trentepohlia or coccoid .......................... 9

10. Ascospores submuriform, clavate, often +/- bent ................ Arthonia interveniens Nyl.

11. Exciple carbonized, at least at the apex ..................................................... 13

12. Disc with a thick, dense white pruina, pruina C+ red (lecanoric acid present) .................. Dyplolabia afzelii (Ach.) A. Massal.

13. Disc variably pruinose, but pruina not thick and dense, C- (lecanoric acid absent) .......... 14

14. 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 inspersed with oil droplets, ............................................... Graphis desquamescens Fée

18. Ascosporo 12-14 celled; common ................................................. 18

19. Ascosporo 6-celled; infrequent .................................................. 19

20. Exciple apically or laterally carbonized (i.e., not carbonized under the hypothecium) ..................................................... 20

21. Exciple smooth, entire, not becoming striate .................. 22

22. Hymenium inspersed with oil droplets .......................... 23

23. Norstictic acid absent (TLC often needed for confirmation) ........................................ 24


26. 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 inspersed  …………………  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 30–65 μm 37–12 l m  ………
   ………  *Graphis striatula* (Ach.) Spreng.
29. Ascospores 15–45 × 6–9 μm  ………  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 .................. 4 3

43. Ascospores large, 1 per ascus, 1-, 80–100 μm long; thallus white, often flaky and appearing sorediate or schizidiate. ..................... Fissurina cypressi (Müll. Arg.) Lendemer

43. Ascospores small, 6-8 per ascus, I- 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 . . . ...................... 4 4

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 ............ 4 5

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 ................................................ 4 6

46. Ascospores muriform; photobiont coccoid ........................................ Arthonia susa R.C. Harris & Lendemer

46. Ascospores transversely septate; photobiont Trentepohlia or coccoid ........................................................ 4 7

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 albovirescens Nyl.

1. Apothecia circular in outline, regular in shape, neither irregular nor elongate ......................................... 4 8

48. Ascospores muriform .......................................................... 4 9

49. Apothecia bright orange, discoid, not opening through a pore .... 5 0

Brigantiaea leucoxantha (Spreng.) R. Sant. & Hafellner

49. Apothecia gray or brown, thelotremoid, opening through a pore. ........................................ 5 1

50. Exciple carbonized, carbonized columella often present. .......... 5 2

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. .......... 5 3

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 .......... 5 4

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 ................................ 5 5

54. Ascospores simple .......................................................... 5 6

55. Asci polysporous; ascospores many per ascus (>100), small globose or ellipsoid .......... 5 7
56. Thallus yellow, K+ purple .......... *Piccolia nannaria* (Tuck.) Lendemer & Beeching
57. 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* Vˇezda
58. 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.
59. Apothecia biauritine, 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* M ¨ull. 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) ............................................. 61

63. Thallus UV+ orange, UV+ dull pink, or UV- ................................................. 63

64. Medulla P+ orange (stictic acid present); ostiole typically raised, resembling a nipple ..... *Pertusaria texana* M ¨ull. 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) ............................................. 64

................................................................. *Pertusaria parataberculifera* Dibben
65. Thallus UV- or UV+ dull pink or orange (thiophanic 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* (F´ee) Nyl.

66. Medulla P- (succinoprotocetraric or stictic acid absent) ...................................... 68

68. Hymenium densely inspersed with oil droplets; warts 
usually sessile ........................................ *Pertusaria sinusmexicanai* Dibben
68. Hymenium not inspersed; 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 (xanthones 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- (xanthones absent) ............................................................ 73

73. Discs densely white pruinose ............................................................ 74

74. Ascospores 8 per ascus, small, <20 \(\mu\)m long ......................................... *Lecanora caesiorubella* Ach. subsp. glaucomodes
74. Ascospores 1-2 per ascus, large, >50 \(\mu\)m 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 .... Variolaia 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...

... Variolaia commutata (Mull. Arg.) ined.

77. Pruina K+ intense yellow slowly turning dirty brown; rare.............................. Variolaia trachythallina (Erichsen) Lendemer et al.

75. Pruina P- (other substances present) .................... 78

78. Pruina K+ lavender (hypothammolic acid present) ...

Variolaia hypothamnolica (Dibben) ined.

78. Pruina K- (hypothammolic acid absent) ............ 79

79. Pruina KC+ violet (picrolichenic acid present) ...........

Variolaia amara Ach.

79. Pruina KC- (picrolichenic acid absent) .......

Variolaia 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; medul- la UV+ blue-white (alectoronic acid present) ...

.......................... Tephromela atra (Huds.) Hafellner

83. Disc reddish-brown; hymenium hyaline; medulla UV- (alectoronic acid absent) ......................... 84

84. Epiphymenium P+ orange-red (pannarin pre- sent); infrequent in inland swamps ........

.......................... Lecanora cinereofusca H. Magn.

84. Epiphymenium P- (pannarin absent); common throughout DRBH .................. 85

85. Disc epruinose; epihymenium with fine POL+ crystals; very common...

... Lecanora hybocarpa (Tuck.) Brodo

(when in doubt, choose this one)

85. Disc weakly white pruinose; epihyme- nium with coarse POL+ crystals; rare

.......................... Lecanora chlorotera Nyl.

69. Apothecia not lecanorine, without a distinct thalline margin .................. 86

69. 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 ...

.......................... Pyrrhospora sp.

88. Thallus continuous, smooth to verruculose; apothecia reddish to tan, highly variable in color, frequently pruinose

.......................... Pyrrhospora varians (Ach.) R.C. Harris
87. Thallus KC-, UV- (xanthones absent) ..................................... 89
89. Thallus scurfy, green, granular, composed of goniocysts; apothecia pallid or tan ................................................. 90
90. Micaeric acid present [TLC required] ......................... 91
90. Methoxymicaeric acid present [TLC required] ..................... 92

................. Micarea microcoeca (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..........

........................... Thalloloma 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 ............ 98

............................. 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 bicolor, 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 .......................................................... 107
107. Apothecia raised, strongly stipitate, with a roughened surface due to the protrusion of paraphyses and asci from the hymenium; infrequent ............

Catinaria atropurpurea (Schaer.) Vězda & Poelt

107. Apothecia not raised and stipitate, with a smooth surface; common .................................. 108
108. Micareic acid present [TLC required] ........

Micarea prasina Fr.

108. Methoxymicareic acid present [TLC required] ........

Micarea 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 ...............

Micarea 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 .............

Micarea 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. Epiphymenium K+ purple; hypothecium orange-brown pigmented, pigment K- ... Bacidia helicospora S. Ekman
117. Epiphymenium 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. Epiphymenium blue-green pigmented; hypothecium and exciple dark purple-brown pigmented; apothecia dark black in color ... Bacidia schueinitzii (Fr. ex Tuck.) A. Schneid.
119. Epiphyllum 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. Epiphyllum 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; epiphyllum

k+ purple........................................

........... **Bacidia helicospora** S. Ekman

121. Apothecia pale, pallid; epiphyllum

k- .............................................................. 122

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. Caceres

127. Ascospores 6-celled; thallus thin, apothecial sessile

.................................................. 128

........... **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
1. Apothecia circular in outline ................................................................. 10

2. Ascospores 4-celled ................................................................. 9

3. Ascospores submuriform to muriform ..................................... 9

4. Hymenium not inspersed; medulla P+ yellow or orange (norstictic and/or stictic acid present); exciple weakly carbonized at the apex, if at all ................................................................. 9

5. Coastal maritime forests; lirellae circular .................................. Phaeographis lobata (Eschw.) Müll. Arg.

6. Inland swamps, often in the canopy; lirellae elongate .................. Phaeographis erumpens (Nyl.) Müll. Arg.

7. Lirellae forming aggregations (pseudostromata) 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 tricosa (Ach.) Müll. Arg.

8. Exciple apically carbonized; rare in DRBH ......................................

9. Ascospores 100–150 µm; lirellae circular, never branching, erumpent and surrounded by ragged bark flaps; restricted to mature maritime forests ................................................................. Phaeographis oricola Lendemer & R.C. Harris

10. Ascospores 16–23 µm; lirellae circular, never branching, erumpent and surrounded by ragged bark flaps; restricted mature maritime forests ................................................................. Phaeographis imshaugiana R.C. Harris

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

12. Ascospores 2-celled ................................................................. 12

13. Ascospores 4-celled; hymenium not inspersed; apothecia lecideine, small; thallus composed of minute green areoles; inland swamps ............................................................. Buellia vernicoma (Tuck.) Tuck.

14. Hypothecium brown ................................................................. 16

15. Thallus K+ yellow turning red, with norstictic acid crystals in section (norstictic acid present) ................................................................. Rinodina dolichospora Malme

16. Amandinea polyspora (Willey) E. Lay & P. May

17. 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 ................................................................. 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*