

1           *Schadonia saulskellyana* (Pilocarpaceae; Lichenized  
2   Ascomycetes) an unusual new species endemic to the southern  
3   Appalachian Mountains of eastern North America

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11       Abstract. – *Schadonia saulskellyana* is described as new to science based on material from  
12 the southern Appalachian Mountains in the eastern United States. The species appears to be  
13 endemic to the region and mostly restricted to the bark of conifers. It is particularly abundant and  
14 frequent in the imperiled high-elevation spruce-fir forests of the region. The new species is  
15 distinguished from its congeners by its corticolous habit, minutely areolate thallus with areoles  
16 that erupt into soralia which dissolve the areoles and give the appearance of a leprose crust,  
17 epruinose, dark brown-black apothecia with a brown hypothecium, and monosporous asci with  
18 large, muriform ascospores. It is also compared with other genera of Pilocarpaceae, particularly  
19 *Calopadia*. *Lopadium disciforme*, a superficially similar species is also compared to the new  
20 species and photographs, as well as a distribution map for eastern North America, are provided for  
21 that species.  
22

23       Keywords. – Biogeography, disjunction, endemism, foliicole, North Carolina, substrate  
24 specificity.  
25

26                   **Introduction**  
27

28       The Appalachian Mountains of eastern North America are a globally recognized  
29 biodiversity hotspot for many organisms including lichens (Lendemer et al. 2014; Tripp &  
30 Lendemer 2019, 2020; Tripp et al. 2019). The exceptional levels of lichen diversity in the region

31 result from a combination of extreme abiotic gradients, prolonged availability for colonization  
32 over geological time, and north-south topographic orientation that facilitated migration during the  
33 last glacial maximum (Dey 1976, 1993; Tripp & Lendemer 2020). High elevation conifer forests,  
34 dominated by red spruce (*Picea rubens*) and the endemic Fraser fir (*Abies fraseri*), are restricted  
35 to the southern portions of the Appalachian Mountains and are among the most iconic Appalachian  
36 ecosystems (Dey 1984). These ecosystems host numerous disjunct and endemic species of plants,  
37 animals and fungi including lichens (Dey 1978). After having been impacted extensively by  
38 historical logging, invasive pathogens and air pollution, the remaining southern Appalachian  
39 spruce-fir forests are now further imperiled by climate change and considered to be critically  
40 endangered (Allen & Lendemer 2016, Lusk et al. 2010, McManamay et al. 2011, Noss et al. 1995,  
41 White et al. 2012).

42 Lichens are among the most biologically diverse and readily visible macroscopic  
43 organismal groups in southern Appalachian spruce-fir forests (Dey 1976, 1993; Tripp & Lendemer  
44 2020). It is thus not surprising that lichens in spruce-fir ecosystems are one of the most intensively  
45 studied lichen cohorts in eastern North America, with multiple taxonomic and floristic accounts  
46 spanning nearly a century (Degelius 1941, Dey 1984, Lendemer et al. 2017). While undescribed  
47 and overlooked lichens continue to be found in these ecosystems, the majority of these appear to  
48 be rare or highly restricted in terms of geographic distribution or ecological niche (Harris et al.  
49 2004; Lendemer & Harris 2013a, b; Lendemer & Tripp 2015; Lendemer et al. 2013). The most  
50 frequent and abundant lichens are instead either species that are broadly distributed across montane  
51 Appalachian ecosystems, widespread temperate eastern North American species, or disjunct from  
52 boreal and Central American montane systems (Dey 1976, 1984).

53 In 2008 the first author made two collections of an unusual crustose lichen in middle and  
54 high elevation habitats of the southern Appalachian Mountains in western North Carolina, U.S.A.  
55 These were characterized by a greenish, granular, sorediate thallus and black, lecideine apothecia  
56 with monosporous asci and hyaline, muriform ascospores. After encountering the species twice, it  
57 was not collected again for over a decade, until the second author found abundantly fertile material  
58 in spruce-fir forests of Grandfather Mountain State Park, North Carolina. All of the collections  
59 were from conifers and led us to question whether it was a previously overlooked rare species of  
60 southern Appalachian lichen communities. We were, nonetheless, perplexed by the gap in

collections, which occurred during a period of intensive study of southern Appalachian lichens in middle and high elevations (e.g., Lendemer 2020, Tripp & Lendemer 2019).

Given that we had multiple well-developed collections of this unidentified lichen, we prepared to describe it as new and compared it to genera that shared the same suite of morphological characters, namely *Calopadia* Vězda, *Lopadium* Körb. and *Schadonia* Körb. By chance, the first author located more abundantly fertile material while carrying out population genetic sampling in the Black Mountains of North Carolina, U.S.A., an area that had been intensively surveyed previously (Lendemer et al. 2017). While only one large fertile thallus was located at that time, numerous thalli without apothecia were located on adjacent trees. This led us to make the connection between our fertile collections, and a nondescript, sterile, granular-sorediate crustose lichen that we had previously found to be frequent in closed-canopy spruce-fir forests. Subsequent careful searching led to the discovery of fertile material at multiple additional locations and the recognition that this highly distinctive species is likely a characteristic member of closed-canopy, southern Appalachian spruce-fir forests. It appears to have previously been overlooked due to the frequent lack of apothecia, and the superficial resemblance of the sterile thallus to the ubiquitous crustose lichen *Bacidia schweinitzii* (Fr. ex Tuck.) A. Schneid. Here we describe this unusual species as *Schadonia saulskellyana*.

## Materials and Methods

This study is based on material deposited in the herbarium of the New York Botanical Garden (NY) collected as part of biodiversity inventory work in the Appalachian Mountains (see Tripp et al. 2019, Tripp & Lendemer 2019). Specimens were first studied dry using an Olympus SZ-STB dissecting microscope and then microscopic morphology and anatomy was then studied with an Olympus BX53 compound microscope. Sections and lichenized diaspore mounts were prepared by hand with a razor blade and mounted in water then treated with K/I, K, nitric acid (HNO<sub>3</sub>) or hydrochloric acid (HCl). Measurements given in the description are either provided as simple ranges of observed values, or as the mean +/- one standard deviation and bounded by the extreme minimum and maximum observed values together with sample size. Chemistry was studied using standard chemical tests (K, C, KC, P, UV) following Brodo et al. (2001) and

supplemented by Thin Layer Chromatography (TLC) using solvent C following Culberson and Kristinsson (1970) but as modified by Lendemer (2011).

### Taxonomic Section

*Schadonia saulskellyana* Lendemer & Hollinger  
MycoBank #846885.

Figures 1–6, 10.

A highly distinctive species of *Schadonia* distinguished from all other members of the genus by its corticolous habit, minutely areolate thallus where soralia erupt from, and dissolve, the areoles into soredia which become confluent and give the appearance of a thick, leprose crust, black apothecia with a dark brown hypothecium, monosporous asci with muriform ascospores, and occurrence at middle and high elevations of the southern Appalachian Mountains in North America.

TYPE: **U.S.A.** North Carolina. Avery Co., Grandfather Mountain State Park, McCrae Peak, along Grandfather Trail ca. 310 m W of summit block at base of series of ladders, 1696 m, massive S-facing granite slab surrounded by *Abies fraseri*-*Betula alleghaniensis* forest, 14 Jul. 2020, on base of young *Abies fraseri*, J.P. Hollinger 24085 (NY!, holotype).

Description. – **Thallus** corticolous, minutely areolate, sorediate, initially forming discrete circular colonies several centimeters in diameter, but these quickly becoming confluent and forming large continuous patches on the substrate; *areoles* minute, weakly corticate, convex, granular in appearance, [44]–(71)–109–(147)–[225]  $\mu\text{m}$  (n=150 from 3 specimens) in diameter, dark green to gray-green in color, erupting into soralia and then almost entirely dissolving into a mass of soredia; cortex poorly developed, a thin layer of irregularly oriented and heavily gelatinized hyphae, POL-; *medulla* thin, a densely packed matrix of irregularly intertwined fungal hyphae and algal cells, POL+ but lacking evident crystals; *soralia* erumpent, diffuse and irregular in shape, rapidly dissolving the areoles to form piles of soredia that become confluent and resemble a leprose thallus; *soredia* fine, [12]–(20.8)–31.3–(41.7)–[60.2]  $\mu\text{m}$  (n=164 from 5 specimens) in

diameter, bright green to green-white in color, often contrasting strongly with the coloration of the undissolved thallus areoles; **apothecia** lecideine, [0.30]–(0.46)–0.63–(0.81)–[1.50] mm (n=100 from 3 specimens) in diameter; *apothecial discs* black, epruinose, smooth, plane to becoming convex and tuberculate, sessile on top of soredia with narrow hyphal attachment in center; *apothecial margin* initially distinct, smooth, concolorous with the disc, epruinose, becoming excluded with age; *epihymenium* unevenly pigmented, reddish-purple to purple-brown, K- or slowly K+ lavender, HNO<sub>3</sub>+ red-purple, not interspersed with crystals or granules, POL-, HCl-; *hymenium* 90–125 µm thick, irregularly streaked with the same pigment as is present in the epihymenium, not interspersed with crystals or oil, POL-; *hypothecium* 100–200 µm thick, dark brown, K- or slowly bleeding yellow, HNO<sub>3</sub>-, HCl- or more vivid red, composed of densely packed intricate hyphae ca. 1.5 µm thick; *exciple* 40–75 µm wide laterally thickening to 100 µm or more near stipe, composed of strongly branched and anastomosing gelatinized hyphae 1.5–2.0 µm wide, internally pigmented with the same pigment as the hypothecium but rapidly transitioning along a gradient to entirely hyaline, not interspersed with crystals or oil, POL-; *paraphyses* weakly branched and anastomosing, [1.0]–(1.2)–1.5–(1.8)–(2.1) µm thick (n=69 from 3 specimens), tips neither expanded nor pigmented; *asci* clavate, with thickened tholus and shallow ocular chamber, outer wall K/I+ blue, inner wall K/I+ blue near tip when immature, with diverging K/I+ blue tubular structure (cf. *Porpidia*-type), [68]–(75)–91–(107)–[130] × [14]–(18)–22–(26)–[30] µm (n=24 from 3 specimens), monosporous to rarely bisporous; *ascospores* hyaline, ellipsoid to oblong, strongly muriform, [35.0]–(44.0)–58.2–(72.5)–[90.0] × [11.7]–(15.5)–17.9–(20.5)–[25.0] µm (n=37 from 5 specimens), all measurements from ascospores outside of asci although these may have been released when the asci were damaged during study; **campylidia** not seen. **Photobiont** green coccoid, cells [3.7]–(4.6)–6.0–(7.2)–[10.3] µm (n=163 from 5 specimens) in diameter.

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

Etymology. – The epithet “*saulskellyana*” honors Mary Sauls Kelly, ecologist and long-time resident of Shelton Laurel in Madison County, North Carolina, U.S.A. Dr. Kelly is a broadly trained naturalist with decades of experience in applied biodiversity assessment and forest management policy, having earned her PhD in ecology from the University of Georgia (Kelly 1988). Much of her career has focused on conservation and sustainable use of southern

Appalachian forests, particularly those in western North Carolina managed as Nantahala and Pisgah National Forests. Through her dynamic engagement as a scientist, advocate, activist and organizer, particularly as the director of the Western North Carolina Alliance—now MountainTrue, she was instrumental in successful grassroots efforts to end large-scale clearcutting projects in the region in favor of practices more compatible with biodiversity and ecosystem health (Newfont 2012). Such practices, combined with preserving large areas of contiguous, high quality forest, are pivotal to maintaining the exceptional lichen biodiversity of the region (e.g., Allen & Lendemer 2016, Tripp et al. 2019), including the habitats where the new species occurs.

Together with her husband Rob Kelly, Dr. Kelly was among the leaders of a coalition to protect Bluff Mountain, a unique area in the Bald Mountains on the North Carolina and Tennessee line that connects disjunct high elevation lichen communities from the Great Smoky Mountains to Unaka and Roan Mountains (Lendemer, unpublished data; see also DePriest 1983). This effort also resulted in founding the Bluff Mountain Music Festival, celebrating both conservation and traditional Appalachian music, held annually in Hot Springs, North Carolina. Currently Dr. Kelly is involved in the Laurel Community Center, an organization that includes STEM education and outreach anchored in aquatic communities of the nearby Laurel River.

Ecology and distribution. – The new species is known from middle and high elevation habitats (3400–6260 ft.; 1036–1908 m.) in the southern Appalachian Mountains of eastern North America from North Carolina north to Virginia, U.S.A (Figure 5). Although described here from a relatively small number of scattered locations, the species is almost certainly more frequent and widespread than the current data suggest. Indeed, once we recognized that it was frequently sterile, we began to locate *Schadonia saulskellyana* in every spruce-fir stand that we visited in the southern Appalachians. In humid, shaded, closed-canopy spruce-fir forests where the boles of Fraser fir are dominated by bryophytes and crustose lichens (Figure 6), *S. saulskellyana* can be among the most common crustose lichens, although most thalli lack apothecia.

The new species occurs almost entirely on the bark of conifers, and the primary phorophytes are Fraser fir and red spruce. At middle elevations in the southern Appalachians, where those tree species do not occur, *Schadonia saulskellyana* was found on two other common and widespread conifers, white pine (*Pinus strobus*) and eastern hemlock (*Tsuga canadensis*). This suggests that although *S. saulskellyana* can occur on a broad range of tree genera, it is nonetheless

184 mostly restricted to conifers. Two collections were made on yellow birch (*Betula alleghaniensis*)  
185 however these were from a stand where the species was otherwise abundant on adjacent red  
186 spruces.

187 Intensive searching of conifer substrates elsewhere in the Appalachian Mountains,  
188 especially in spruce-dominated forests of the central Appalachians of Virginia and West Virginia,  
189 is needed to confirm that the species is endemic to the southern Appalachians. Nonetheless, there  
190 are data that support the status of *S. saulskellyana* as a regional endemic primarily restricted to  
191 high elevation spruce-fir forests. First, during the writing of this paper, the authors and their  
192 colleagues studied balsam fir (*Abies balsamea*) stands in Shenandoah National Park, Virginia and  
193 several red spruce dominated stands in West Virginia (e.g., Gaudineer Knob, Spruce Knob) where  
194 the species was not located. While in contrast, the species was located at additional red spruce or  
195 Fraser fir-red spruce sites in Virginia where it had not been collected previously by others (e.g.,  
196 Balsam Beartown Mountain, Mount Rogers, Whitetop Mountain). This suggests the species occurs  
197 in stands with Fraser fir but not those with balsam fir, The occurrence on Beartown Mountain in  
198 a pure red spruce stand is an outlier. Second, extensive fieldwork at middle and low elevations of  
199 the southern Appalachians during the last decade has also failed to locate additional occurrences  
200 of the species. This suggests that although *S. saulskellyana* can occur in middle elevation habitats  
201 of the region, it is likely much rarer there in comparison to high elevation spruce-fir forests.  
202 Finally, northwards in the Appalachian Mountains and related ranges in New England, the species  
203 does not appear to have been encountered despite nearly two centuries of study that has particularly  
204 emphasized conifer forests and high elevation habitats (e.g., Seaward et al. 2017, Selva 1994,  
205 Tuckerman 1847).

206  
207 Discussion. – We considered a wide range of potential genera to which the new species  
208 could belong. The apothecial pigment, particularly the dark brown hypothecium (Figures 3, 4A-  
209 C), combined with the monosporous asci and large, hyaline, muriform ascospores (Figures 4I-L)  
210 strongly suggested *Lopadium*, *Calopadia* or *Schadonia*. *Lopadium* is similar in these respects, but  
211 differs from the material of the new species in having a persistent, well-developed apothecial  
212 margin (vs. margin that is soon excluded), asci that lack a distinct tholus (vs. with a distinct tholus),  
213 and most notably in having relatively thick paraphyses with a conspicuous spike-like or conical,  
214 dark pigmented cap on the uppermost cells (vs. very narrow paraphyses that lack pigment caps)

(Döbbeler et al. 1985, Hafellner 1984, Smith et al. 2009; compare Figures 1 and 4 of *S. saulskellyana* with Figure 7 of *L. disciforme* herein). The only species of *Lopadium* that occurs in the southern Appalachian Mountains is *L. disciforme* (Flot.) Kullh. (Tripp & Lendemer 2020) and *L. disciforme* occurs in the same habitats and on the same substrates as the new species. However, in addition to the characters listed above, *L. disciforme* differs markedly from the new species in having a well-developed, areolate, esorediate thallus (compare Figures 1E&F, and 2 of *S. saulskellyana* with Figures 7A&B of *L. disciforme* herein).

*Calopadia* is one of several genera, such as *Brigantiaea* Trevis. and *Tapellaria* Müll. Arg., that were previously included within a broadly delimited *Lopadium* based on their large, muriform ascospores (Santesson 1952, Vězda 1986). As has been outlined in multiple publications (e.g., Döbbeler et al. 1985; Hafellner 1984, 1997; Kalb & Vězda 1987), these genera differ in many respects from the small group of species that comprise *Lopadium* s. str., including its type *L. pezizoideum* (Ach.) Körb. which occurs on soil the arctic (Brodo et al. 2001) and *L. disciforme* which occurs on bark in wet, northern temperate and boreal regions of the Northern Hemisphere and has an Appalachian-Great Lakes Distribution in eastern North America (Brodo et al. 2001; Figure 8 herein). The new species does not match the current delimitation of *Tapellaria* as that genus differs in having lecideine apothecia with a dark brown-black pigmented exciple (vs. internally brownish but rapidly transitioning outward to hyaline in our material) (Lücking 2008). Similarly, it does not match the current delimitation of *Brigantiaea* in numerous respects, most notably the absence of anthraquinones in the apothecia (Hafellner 1997). Many morphological characters of the new species are in agreement with *Calopadia*, even though campylidia, highly distinctive conidium bearing structures, were not found in our material and our material was from habitats more similar to those of northern temperate or boreal regions rather than the tropical habitats typical of *Calopadia* (Lücking 2008, Sanders 2014). It has however, been noted previously that corticolous thalli of normally foliicolous *Calopadia* species often lack campylidia (Cáceres 2007). Despite the morphological similarities to *Calopadia*, our material differs from that genus in the anatomy of the exciple. *Calopadia* has a paraplectenchymatous exciple composed of large, thin-walled, isodiametric cells (Figure 9). *Schadonia saulskellyana* has a prosoplectenchymatous exciple composed of branched and anastomosing, narrow hyphae in a thick gelatinous matrix (Figure 10).

*Schadonia* is a small genus of three species, with a fourth Brazilian species, *S. subobscurata* (Vain.) Kalb, having been transferred to *Brigantiaea*, as *B. subobscurata* (Vain.) Aptroot (Aptroot 2002). Two of the species, *S. alpina* Körb. and *S. fecunda* (Th. Fr.) Vězda & Poelt appear to be rare, primarily not corticolous (mostly terricolous, saxicolous or muscicolous), occur in alpine or boreal habitats of Europe (Poelt & Vězda 1981) and have been reported from North America (Esslinger 2021). A third species, *S. indica* Upreti & Nayaka, is corticolous and so far, known only from India (Upreti & Nayaka 2006).

Although no detailed treatment of *Schadonia* has been published to date, the apothecium morphology of the new species, including the prosoplectenchymatous exciple and asci with a distinct amyloid tholus, match well those of the European species (e.g., Ekman 1996, Poelt & Vězda 1981; compare Figures 3, 4 and 10 of *S. saulskelleyana* to Figure 11 of *S. fecunda* herein). The presence of the new species in high elevation spruce-fir habitats, which include many floristic elements typical of northern boreal and arctic regions (Lendemer et al. 2017, Tripp & Lendemer 2019), also agrees with *Schadonia*. The primary morphological difference between the new species and all known *Schadonia* is that it has predominantly monosporous asci while those of *Schadonia* uniformly produce two or more ascospores per ascus (2–4 in *S. alpina*, 8 in *S. fecunda* and *S. indica*; Poelt & Vězda 1981, Upreti & Nayaka 2006). The strictly corticolous, or rarely lignicolous, habit is also very different from the ecology of *S. alpina* and *S. fecunda*, both of which are typical of alpine humus or soil communities (Poelt & Vězda 1981). Given the preponderance of morphological and biogeographic similarity, we describe the new species in *Schadonia* with the recognition that it may eventually be better placed in another genus when molecular data become available. It should be noted that as of the writing of this text, only two sequences of *Schadonia* were available in GenBank (mtSSU: AY756376, nucLSU/28S: AY756362; both generated nearly two decades ago).

While apothecium anatomy and biogeography suggest a placement in *Schadonia*, the new taxon is much more likely to be confused with one of the many described *Calopadia* species. Although there are more than twenty species of *Calopadia*, the majority of these are foliicolous, have smooth thalli and frequently produce campylidia, hence they are not likely to be confused with *S. saulskelleyana* (Lücking 2008). No other members of the genus are known to occur on bark in middle and high elevation habitats in the southern Appalachian Mountains (e.g., Lendemer et al. 2017; Tripp & Lendemer 2019, 2020). The only other *Calopadia* species known from the region

is the foliicolous *C. puiggarii* (Müll. Arg.) Vězda, which differs in having lighter colored, gray-brown apothecia and a smooth, continuous thallus (Lücking 2008). In the Appalachians, that species is restricted to the leaves of evergreen shrubs, especially *Leucothoe* and *Rhododendron*, in very high humidity riparian corridors at low and middle elevations (J. Hollinger & J. Lendemer, unpublished data). *Calopadia puiggarii* is one of a cohort of foliicolous species with primarily tropical or subtropical distributions and that are disjunct between the Coastal Plain of southeastern North America and riparian corridors at middle and low elevations of the southern Appalachians (Sérusiaux 1979, Tripp & Lendemer 2019; Figure 12 herein).

Based on the epithet, we considered that the new species might be similar to *Calopadia granulosa* Aptroot & M. Cáceres, a corticolous species that is known only from rainforests in Brazil. However, *C. granulosa* has a very different corticate thallus that appears to be verruculose or coarsely granular rather than sorediate, reddish-brown apothecia with light brown margins, and smaller ascospores ( $33\text{--}38 \times 10.5\text{--}13.0\text{ }\mu\text{m}$ ; Aptroot & Cáceres 2014: 784, figs. 1A-C). As was noted by Aptroot and Cáceres (2014) there are only two other species of *Calopadia* with thalli that are not continuous and smooth, and while both are evidently corticolous, they differ significantly from *S. saulskellyana* in that *C. insidiosa* Kalb & Vězda has an isidiate thallus, while *C. psoromoides* Kalb & Vězda has a squamulose thallus (Kalb & Vězda 1987).

Most other known corticolous species of *Calopadia* with muriform ascospores differ markedly from *S. saulskellyana* in having a smooth, continuous thallus and pruinose apothecia (e.g., *C. bonitensis* M. Cáceres & Lücking, see Cáceres 2007; *C. cinereopruinosa* Bungartz & Lücking and *C. editiae* Vězda ex Chaves & Lücking, see Lumbsch et al. 2011; *C. perpallida* (Nyl.) Vězda, see Lücking 2008; *C. schomerae* Seavey & J. Seavey, see Seavey & Seavey 2011). One exception is *C. subfusca* Kalb & Vězda, which was described based on corticolous material and has subsequently been reported to also be foliicolous (Lücking 2008). Confusion of the new species with *C. subfusca* is unlikely since that species has brown rather than black apothecia, the thallus is continuous and smooth, and the ascospores are 2–4 per ascus (Kalb & Vězda 1987). *Calopadia subcoerulescens* (Zahlbr.) Vězda is another species that can be both corticolous and foliicolous, and has epruinose apothecia, but it differs from the new species in having a smooth, continuous thallus and apothecia with an aeruginose pigmented hypothecium (Lücking 2008). *Calopadia lecanorella* (Nyl.) Kalb & Vězda is tropical species similar to *S. saulskellyana* in being corticolous and having black apothecia as well as monosporous asci with muriform ascospores of

a comparable size (Kalb & Vězda 1987). Nonetheless that species is reported to have a smooth, thin thallus and campylidia are known (Kalb & Vězda 1987).

Much as we did, the average person in the field would likely overlook *Schadonia saulskellyana* and assume that it was poorly developed material of other common and widespread Appalachian species. *Bacidia schweinitzii* is the most superficially similar species, and the small, black apothecia of *S. saulskellyana* would likely be confused with either the large pycnidia or immature apothecia that are typical of some forms of *B. schweinitzii* (Ekman 1996, Harris & Ladd 2015, Lendemer et al. 2016). That species differs from *S. saulskellyana*, however, in having an esorediate thallus and acicular, needle-like ascospores (Ekman 1996, Lendemer et al. 2016). It also differs chemically in the production of atranorin, although that substance can usually only be detected with thin layer chromatography (Lendemer et al. 2016). Ecologically *B. schweinitzii* also differs in almost never occurring on red spruce or Fraser fir, although it does occur on other conifers at middle and low elevations (Lendemer et al. 2016).

The new species could also be confused with members of the *Micarea prasina* group, whose thalli often form extensive, brownish-green or vibrant grass-green colored colonies on bark in closed-canopy southern Appalachian spruce-fir forests (Tripp & Lendemer 2020). Most members of that group have a thallus that is composed of goniocysts rather than granular soredia, differ chemically in the production of micareic or methoxymicareic acid, and are frequently fertile with tan to dark-brown apothecia and simple to 2-celled ascospores (Barton & Lendemer 2014, Guzow-Krzemińska et al. 2019, Launis et al. 2019). *Micarea soralifera* Guzow-Krzem., Czarnota, Łubek & Kukwa is a sorediate member of the *M. prasina* group that can resemble *S. saulskellyana* from a distance. While *M. soralifera* also grows on conifers, it is mostly restricted to middle and low elevations in the southern Appalachians and differs chemically from *S. saulskellyana* in the presence of micareic acid (Guzow-Krzemińska et al. 2016).

*Ropalospora viridis* is another sorediate lichen with a dark greenish or brownish-green thallus that also occurs in southern Appalachian spruce-fir forests with *Schadonia saulskellyana* (Tripp & Lendemer 2020). Unlike *S. saulskellyana*, *R. viridis* is typically found on hardwoods and the branches of conifers (vs. the trunks) and it has a thick, relatively continuous thallus that regularly forms small circular rosettes, and often has a conspicuous shiny brown prothallus (Lendemer 2011, Tønsberg 1992). *Ropalospora viridis* also differs from *S. saulskellyana* in the production of perlatolic acid (Lendemer 2011).

339        *Additional specimens examined.* – U.S.A. North Carolina. Clay Co., Nantahala National  
340 Forest, stream bed/valley of Buck Creek, 1–1.5 mi N of US64 on Buck Creek Rd., 10 Nov. 2007,  
341 on *Tsuga*, J.C. Lendemer et al. 10489 (NY); Buck Creek Barrens, 10 Nov. 2007, on *Tsuga*, S.Q.  
342 Beeching 4390 (NY). Haywood Co., Great Smoky Mountains National Park, Cataloochee Balsam,  
343 N side of Polls Gap trail near W end of mountain ca. 3.0 km N of Polls Gap trailhead, 31 May  
344 2022, on *Picea*, J.P. Hollinger 27096 (NY); Great Smoky Mountains National Park, Big  
345 Cataloochee Mountain, along Sterling Ridge Trail ca. 1.6 mi E of Balsam Mountain Trail, on  
346 *Picea*, J.P. Hollinger 27531 & P.A. Scott (NY); Great Smoky Mountains National Park, Gunter  
347 Fork Trail, 0.2–0.4 mi from top, on *Betula alleghaniensis*, J.P. Hollinger 27561 & P.A. Scott (NY),  
348 J.P. Hollinger 27563 & P.A. Scott (NY), on *Picea*, J.P. Hollinger 27562 & P.A. Scott (NY), on  
349 *Tsuga*, J.P. Hollinger 27574 & P.A. Scott (NY); Great Smoky Mountains National Park, Baxter  
350 Creek Trail, ca. 1 mi from the top, on *Picea*, J.P. Hollinger 27626 & N.L. Noell (NY), J.P.  
351 Hollinger 27629 & N. Noell (NY). Macon Co., Highlands Ravenel Park, trail to Sunset Rock, 30  
352 Apr. 2006, on *Pinus*, J.C. Lendemer et al. 7030 (NY). Swain Co., Great Smoky Mountains  
353 National Park, Cataloochee Balsam, just above old Polls Gap Trail near E end of mountain ca. 2.2  
354 km N of Polls Gap trailhead, 31 May 2022, on *Picea*, J.P. Hollinger 27108 (NY); Great Smoky  
355 Mountains National Park, Balsam Mountain Trail between Tricorner Knob and Luftee Knob, ca.  
356 1.5 mi E of Appalachian Trail, on *Picea*, J.P. Hollinger 27480 & P.A. Scott (NY). Yancey Co.,  
357 Pisgah National Forest, Black Mountains, E-slopes just S of Black Mountain Crest Trail and Big  
358 Tom Trail, ~0.4 mi N of Big Tom summit, 27 Oct. 2021, on *Abies*, J.C. Lendemer et al. 71948  
359 (NY). Tennessee. Sevier Co., Great Smoky Mountains National Park, Sweet Ridge, ca. 2.2 mi  
360 from Mt. Collins shelter N bound on Sugarland Mountain Trail, 29 Sep. 2021, on *Picea*, J.P.  
361 Hollinger 26062 (NY); Great Smoky Mountains National Park, False Gap, on *Abies*, J.P.  
362 Hollinger 27190 (NY); Great Smoky Mountains National Park, Porters Gap, on *Picea*, J.P.  
363 Hollinger 27202 (NY), J.P. Hollinger 27203 (NY); Great Smoky Mountains National Park, Eagle  
364 Rocks, on *Picea*, J.P. Hollinger 27225 (NY); Great Smoky Mountains National Park, Hughes  
365 Ridge, ca. 1.8 km S of Pecks Corner Shelter, on *Picea*, J.P. Hollinger et al. 27236 (NY); Great  
366 Smoky Mountains National Park, Appalachian Trail near Pecks Corner, on *Picea*, J.P. Hollinger  
367 27391 & P.A. Scott (NY); Great Smoky Mountains National Park, Mount Sequoyah, on *Picea*,  
368 J.P. Hollinger 27396 & P.A. Scott (NY); Great Smoky Mountains National Park, Appalachian

Trail between Tricorner Knob and Mount Guyot, on *Picea*, J.P. Hollinger 27431 & P.A. Scott (NY), J.P. Hollinger 27360 & P.A. Scott (NY), J.P. Hollinger 27465-a & P.A. Scott (NY); Great Smoky Mountains National Park, S slope of Mount LeConte, Alum Cave Trail ~1 mi SE of LeConte Lodge, upper slopes of Huggins Hell above headwaters of Styx Branch, 2 Aug. 2022, on *Picea*, J.C. Lendemer et al. 77167 (NY). Virginia. Grayson Co., Jefferson National Forest, Mount Rogers National Recreation Area, Lewis Fork Wilderness, S-facing slopes of Mount Rogers, 16 Apr. 2022, on *Abies* base, J.C. Lendemer et al. 73072 (NY), on *Picea*, J.C. Lendemer et al. 73091 (NY), J.C. Lendemer et al. 73092 (NY). Smyth Co., Jefferson National Forest, W-slopes below summit of Whitetop Mountain, 15 Oct. 2022, on *Picea*, J.C. Lendemer 75454 & J.W. Howland (NY), J.C. Lendemer 75455 & J.W. Howland (NY), on log, J.C. Lendemer 75517 (NY). Tazewell Co., Jefferson National Forest, Beartown Wilderness, Garden Mountain, Beartown Ridge, 20 Oct. 2022, on *Picea*, J.C. Lendemer et al. 76230 (NY).

## Conclusion

The discovery and recognition of *Schadonia saulskellyana* in the southern Appalachian Mountains of eastern North America further highlights the remarkable heterogeneity of biogeographic elements present in the region (Hedin & McCormack 2017, Manos & Meireles 2015, White et al. 1984; for lichens see Tripp & Lendemer 2019). Interestingly, the new species appears to be an endemic that is morphologically and ecologically incongruous with its congeners in having an areolate, sorediate thallus and corticolous habit, monosporous asci, and in being strongly disjunct from the alpine boreal habitats that characterize *S. alpina* and *S. fecunda* (Lücking 2008). It is also noteworthy that in a biodiversity hotspot where narrowly endemic vascular plants and animals are distributed across many ecosystems and elevations (Davies 1955, Estill & Cruzan, 2001, Hedin & McCormack 2017, Niemiller & Zigler 2013, Petranksa 1998), the new species adds to the growing body of literature that suggests most strictly southern Appalachian lichen endemics occur as naturally fragmented, disjunct populations largely restricted to high elevation ecosystems (Allen & Lendemer 2016, Allen et al. 2018, Lendemer & Allen 2015, Lendemer & McMullin 2022, Tripp & Lendemer 2019).

That the species was largely overlooked in the ecosystems, and on the substrates, where it is most frequent, is remarkable considering the amount of lichen biodiversity inventory work that

has been carried out across the southern Appalachians for well over two decades (Allen & Lendemer 2016; Lendemer et al. 2013, 2017; Tripp & Lendemer 2019, 2020). It is even more remarkable that some of the locations where the species was found, and found growing abundantly, were among areas that had already been visited multiple times by the authors previously (e.g., Cataloochee Balsam and Mount Collins in Great Smoky Mountains National Park, or Big Tom in the Black Mountains). This starkly illustrates the detection-, and collection-, bias that exists for crustose lichens with dominantly asexual reproductive modes even when specialists in these very taxa lead the inventory efforts[!]. Concurrently it underscores that iterative, intensive, and repeated study is required to develop a clear understanding of the ecology, distribution and morphological variation of crustose microlichens that have previously been little studied (Lendemer 2021). This is particularly poignant in the broader context of attempting to conserve understudied biodiverse groups in areas that are currently undergoing rapid, ecosystem-wide change (Allen et al. 2019).

### Acknowledgments

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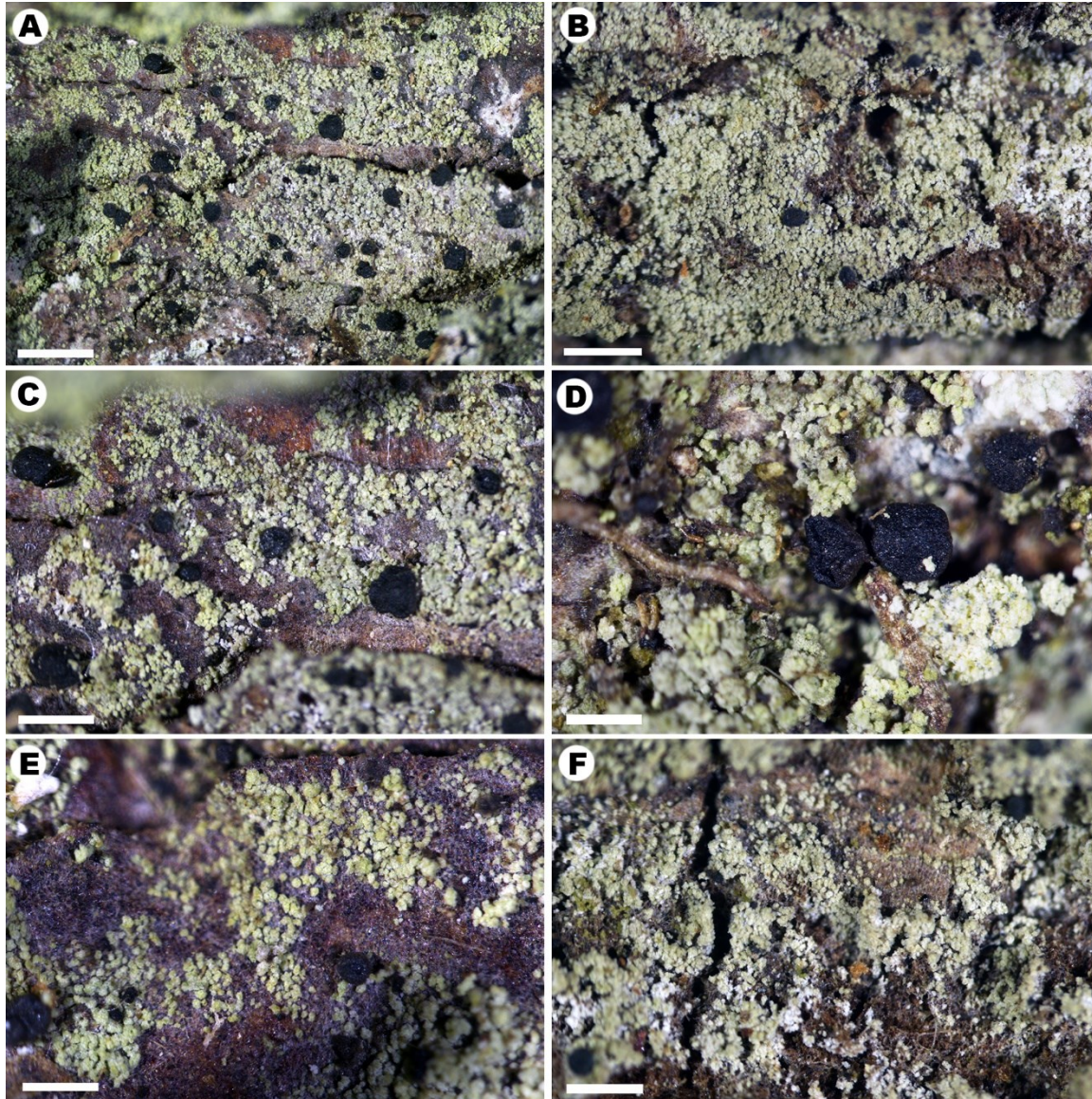


Figure 1. Morphology of *Schadonia saulskellyana* (A, C, and D from *Hollinger 24085*, holotype; B, E and F from *Lendemer 10489*). A-C, gross morphology of the thallus and apothecia. D, detail of apothecial variation and areoles dissolving into soredia. E, detail of areoles prior to formation of soralia. F, detail of portion of thallus where areoles have nearly completely dissolved into soredia. Scales = 2.0 mm in A and B, 1.0 mm in C, 0.5 mm in D-F.

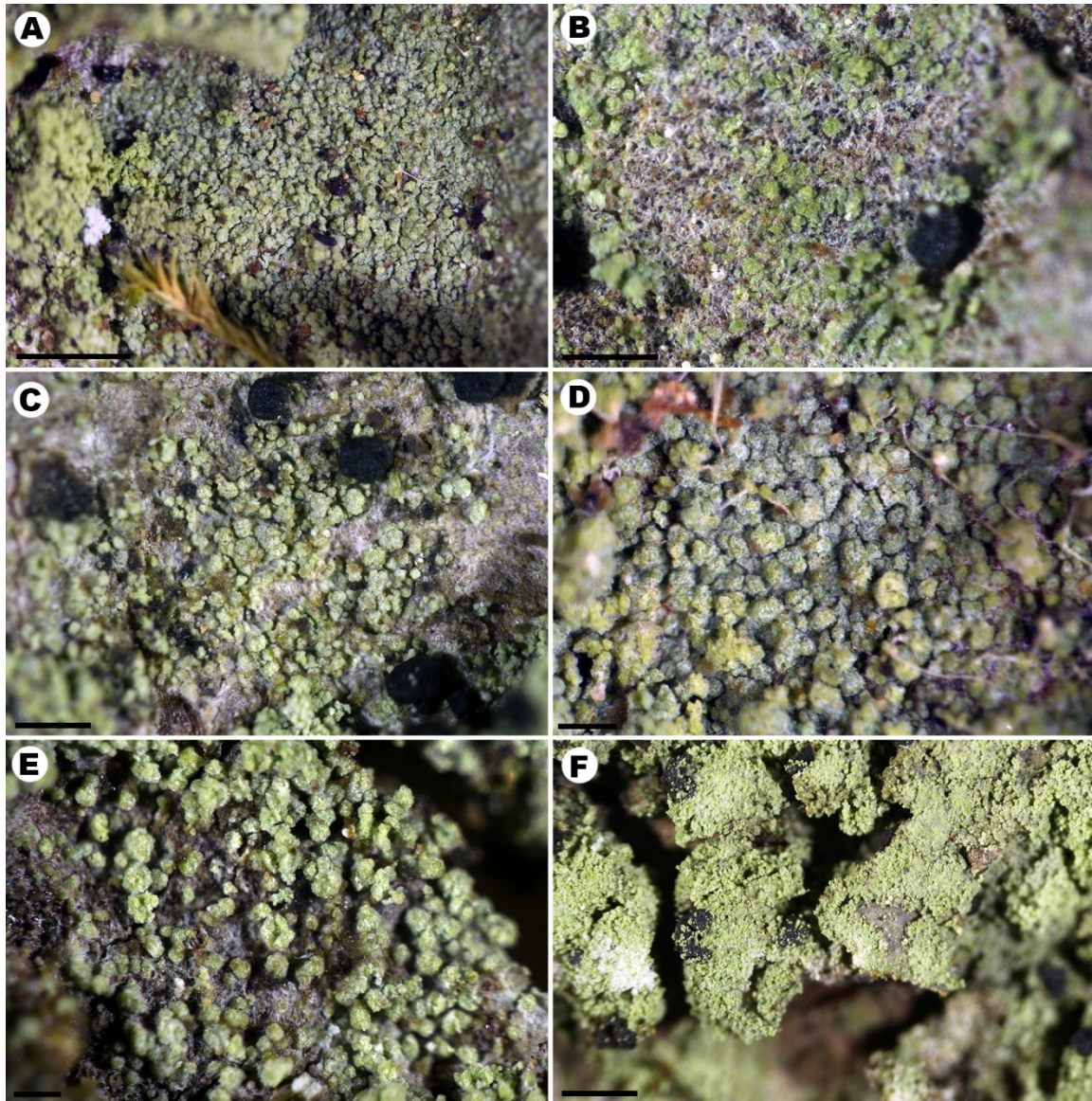


Figure 2. Thallus development in *Schadonia saulskellyana* (A & F from *Lendemer 71948*, B & E from *Lendemer 73091*, C & D from *Lendemer 73072*). A, intact thallus areoles with early stages of soralium formation viewed from a distance. B, detail of young, flattened areoles, beginning to become convex. C, mature thickened areoles beginning to form erumpent soralia. D, contiguous areoles with some erumpent soralia. E, somewhat dispersed areoles with well-developed erumpent soralia. F, thallus completely dissolved in soredia giving the appearance of a leprose crust. Scales = 1.0 in A & F; 0.5 mm in B, C & E; 0.2 mm in D.

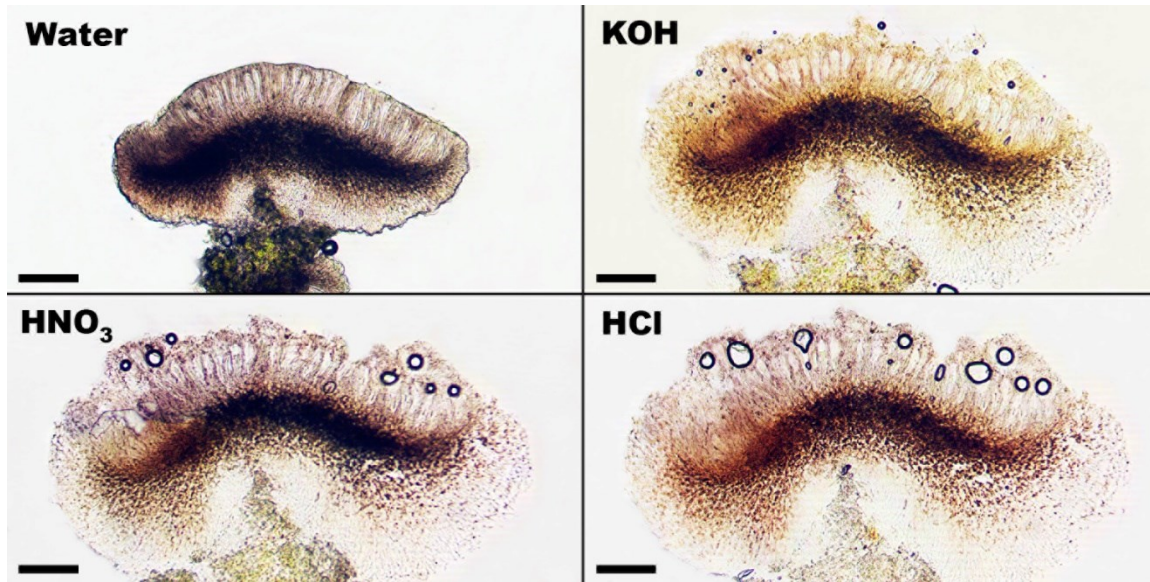
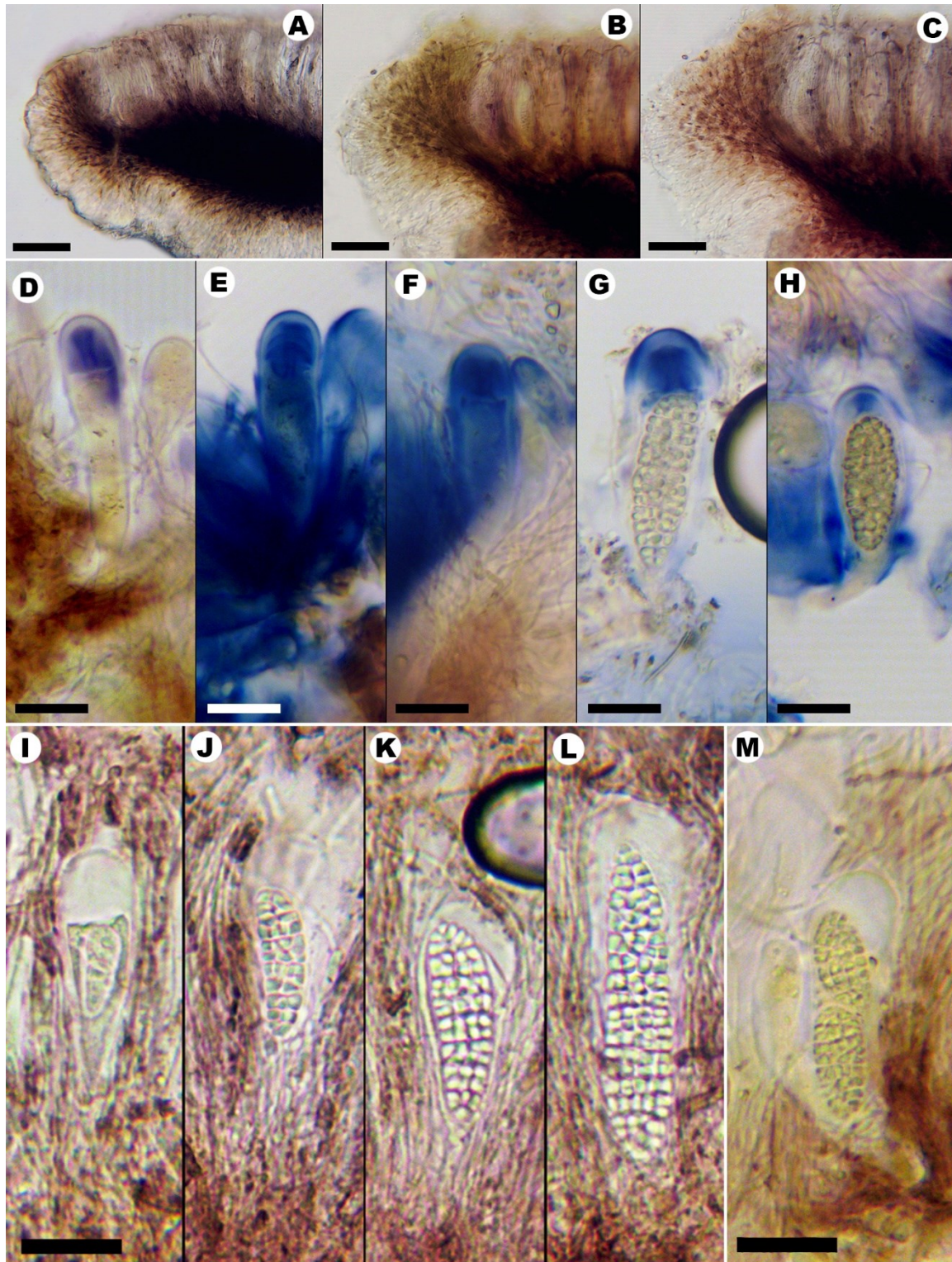


Figure 3. apothecial anatomy and pigmentation in *Schadonia saulskellyana* (from Hollinger 24085, holotype) as viewed in a section of an apothecium in water, 10% potassium hydroxide (KOH), 10% nitric acid (HNO<sub>3</sub>) and 10% hydrochloric acid (HCl). Scales = 100 μm.



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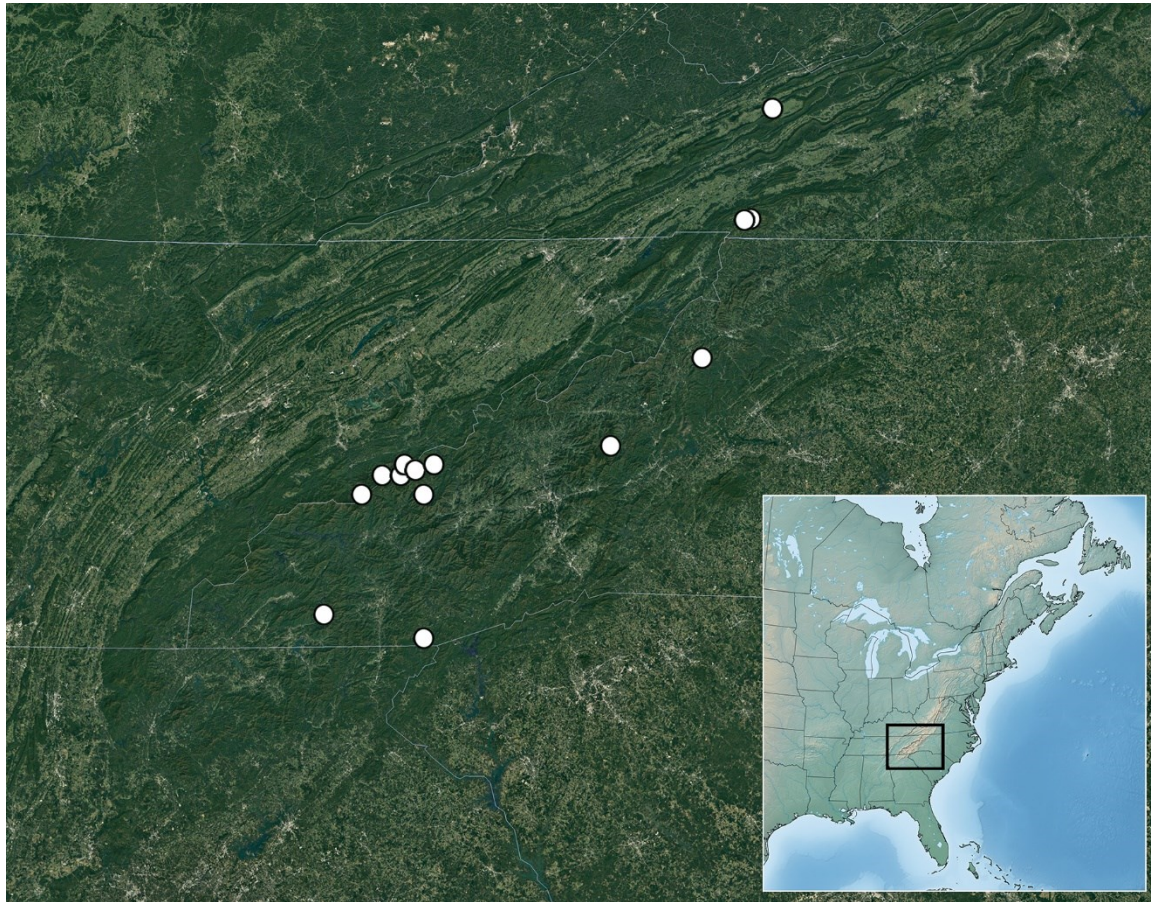
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Figure 4. Apothecial anatomy of *Schadonia saulskellyana*. (A-H & M from *Hollinger 27096*, I-L from *Hollinger 24085*, holotype). A-C, detail of transverse section of apothecium illustrating pigmentation and excipular anatomy in water (A), KOH (B) and nitric acid (C). D-H, ascus

644 anatomy and staining of the tholus in K/I. I-L, ascus and ascospore development. M, atypical  
645 bisporous ascus in KOH. Scales = 50  $\mu\text{m}$  in A-C, 20  $\mu\text{m}$  in D-M.



646  
647 Figure 5. Geographic distribution of *Schadonia saulskellyana* based on specimens examined for  
648 this study. Area depicted with satellite imagery is bounded in a black box in the inset.  
649

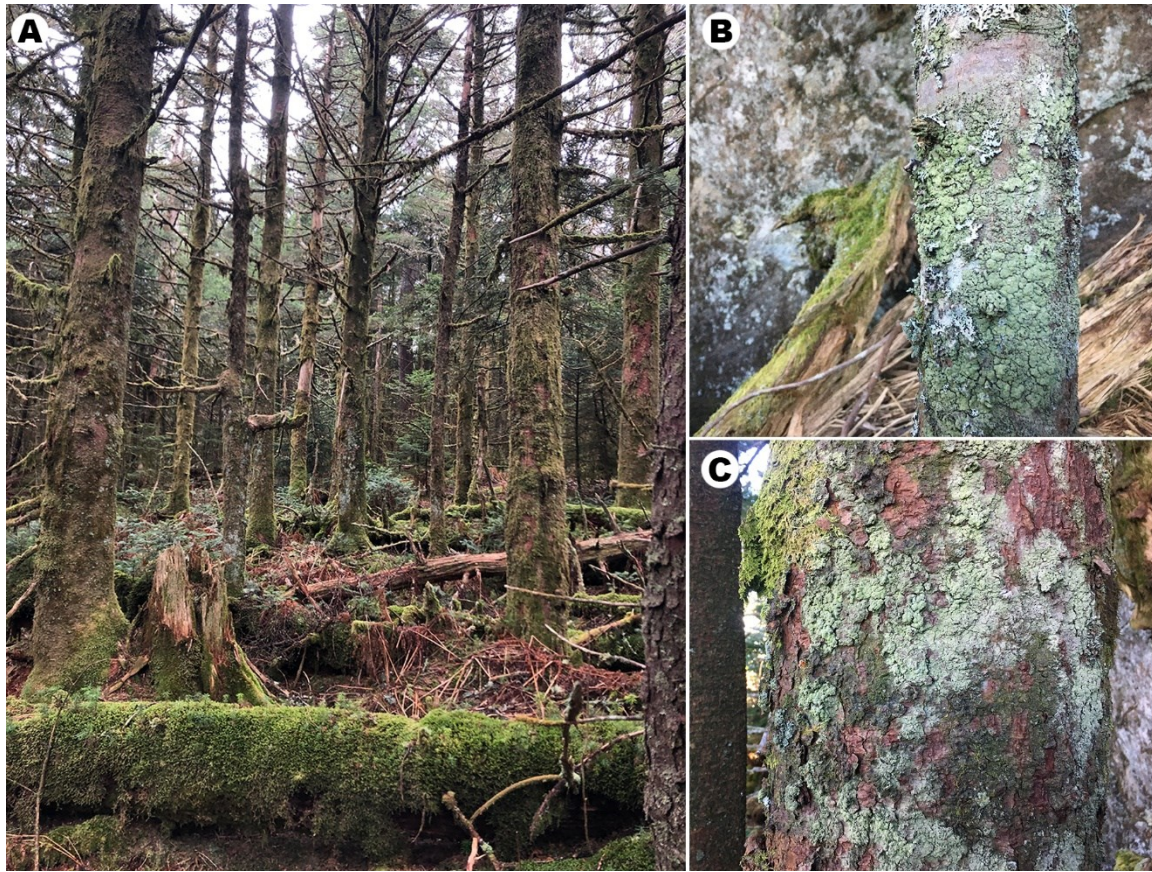


Figure 6. Ecology of *Schadonia saulskellyana*. A, typical spruce-fir forest habitat (summit of Mount Rogers, Virginia, U.S.A.). B, fertile thallus on young Fraser fir (Big Tom, Black Mountains, Pisgah National Forest, North Carolina, U.S.A.). C, sterile thallus on mature Fraser fir (Cattail Peak, Black Mountains, Pisgah National Forest, North Carolina, U.S.A.).

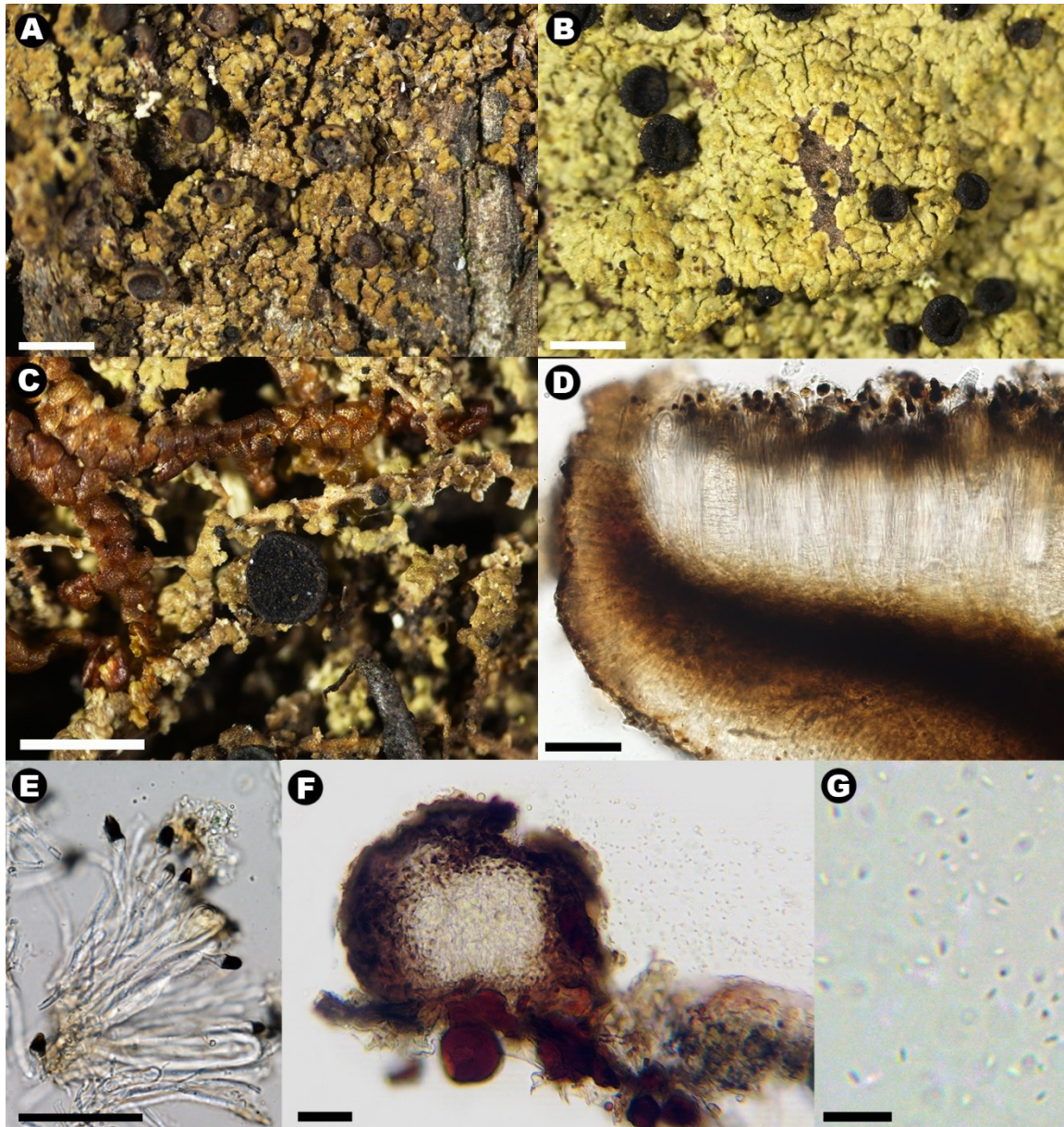
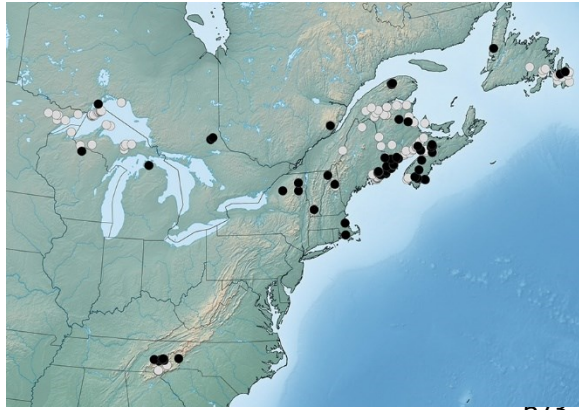


Figure 7. Morphology and anatomy of *Lopadium disciforme* (A from *Lendemer* 43271, B from *Lendemer* 44182, C from *Lendemer* 46162, D & E from *Lendemer* 23050, F & G from *Hollinger* 24272). A and B, gross morphology of thallus. C, detail of mature apothecium with persistent margin. D, transverse section of apothecium illustrating pigmentation and anatomy, particularly of the exciple. E, detail of paraphyses illustrating conspicuous black pigment caps. F, transverse section of a pycnidium. G, conidia. Scales = 1.0 mm in A and B, 0.5 mm in C, 50  $\mu$ m in D and E, 25  $\mu$ m in F, 5  $\mu$ m in G.

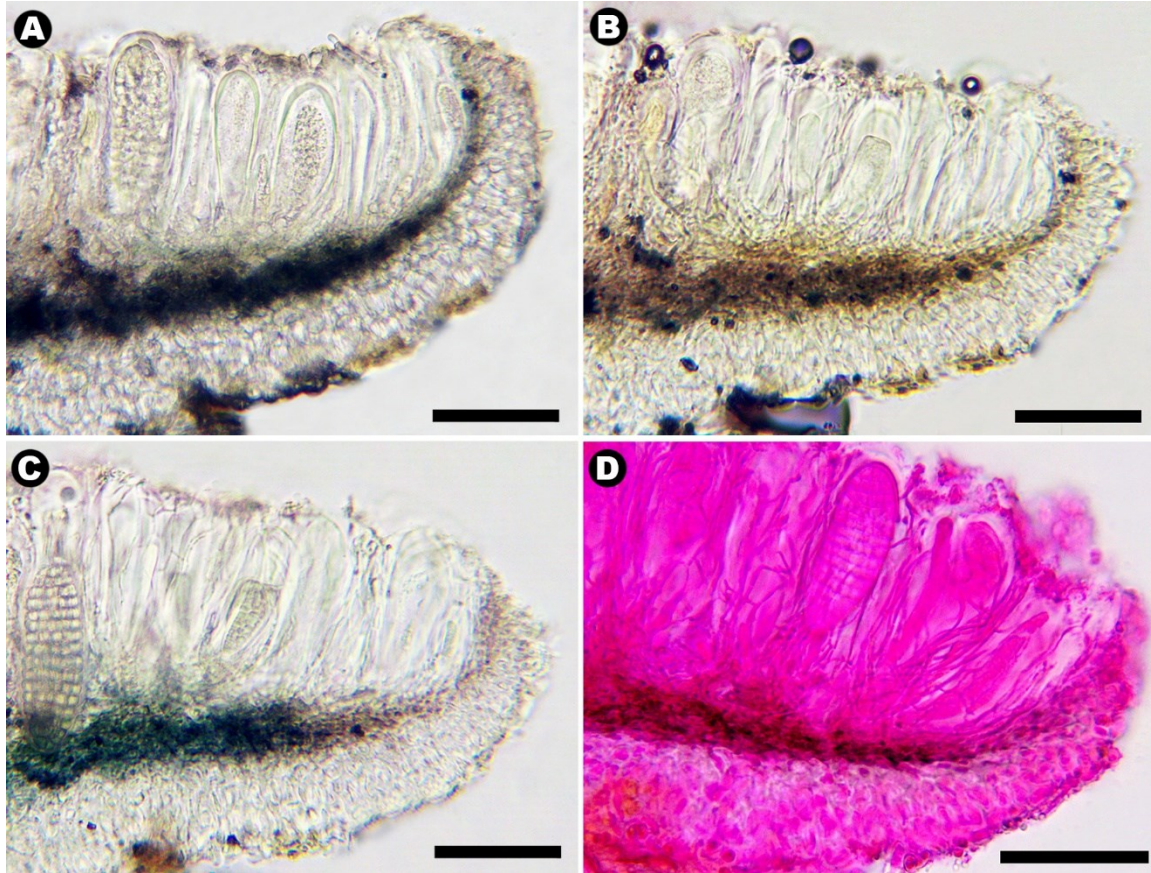


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677 Figure 8. Geographic distribution of *Lopadium disciforme* in eastern North America based on  
678 specimens examined for this study at NY (black) and records from CNALH (gray).



679

680 Figure 9. Transverse sections of apothecium of *Calopadia puiggarii* (all from *Hollinger 23994*)

681 illustrating pigmentation and excipular anatomy in water (A), potassium hydroxide or KOH (B),

682 nitric acid or N (C), and stained in phloxine after treatment with KOH (D). Scales = 50  $\mu$ m.

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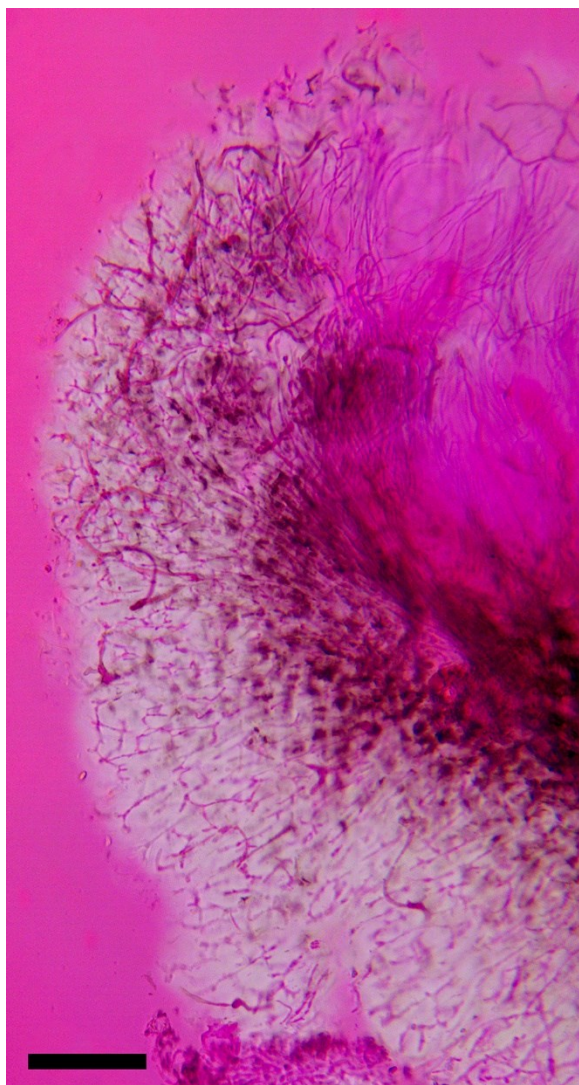


Figure 10. Detail of excipular anatomy in *Schadonia saulskellyana* illustrating the prosoplectenchymatous exciple composed of branched and anastomosing, narrow hyphae in a thick gelatinous matrix (from *Hollinger 27096*) as viewed in a transverse section stained in phloxine after treatment with KOH. Scale = 20  $\mu\text{m}$ .

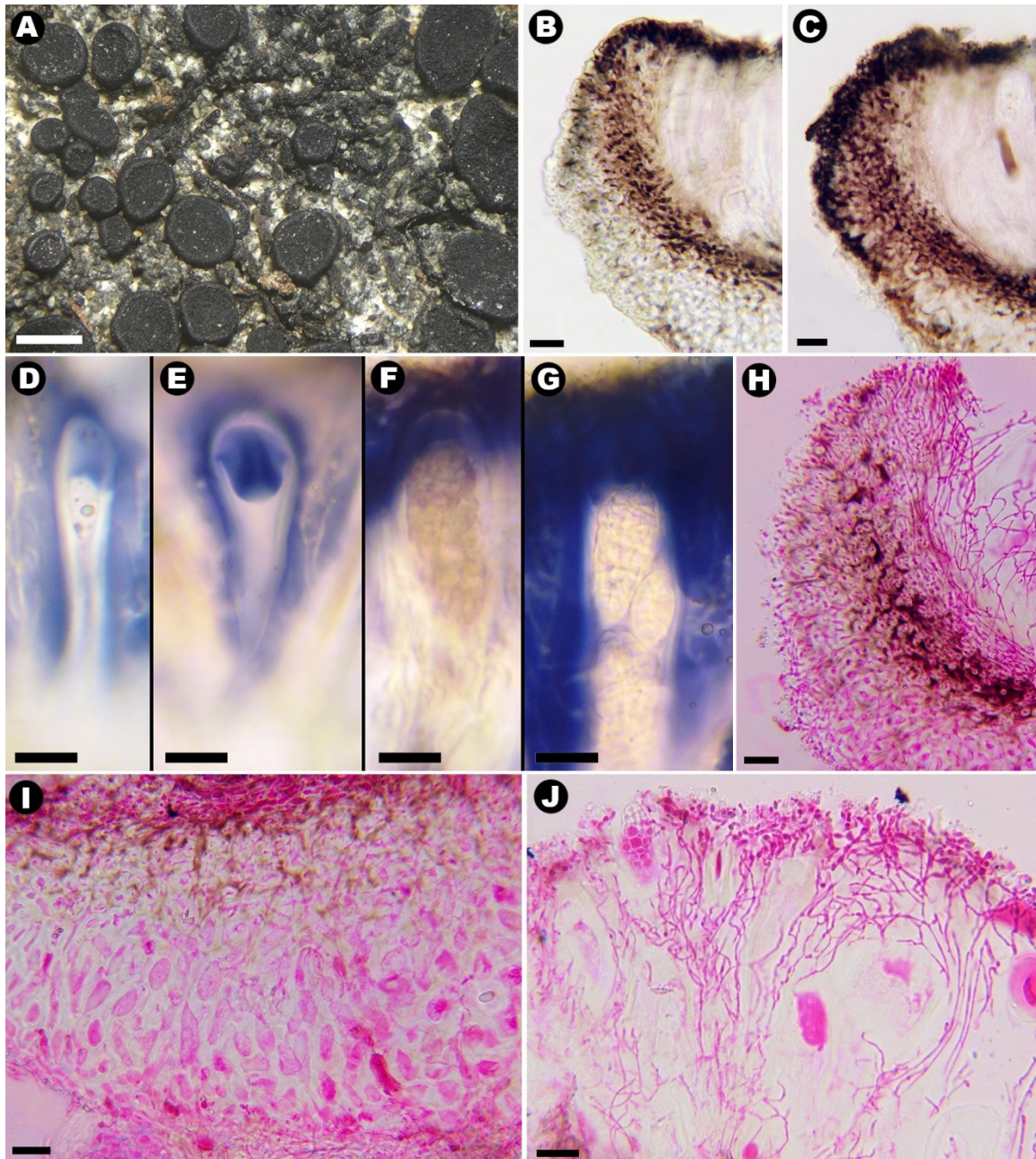


Figure 11. Morphology of *Schadonia fecunda* (all from Fryday 8345, MSC). A, gross morphology of the apothecia. B, exciple mounted in water. C, exciple mounted in KOH. D-G, asci mounted in K/I. H, exciple stained with phloxine. I, detail of lower exciple stained with phloxine. J, paraphyses stained with phloxine. Scales = 0.5 mm in A, 25  $\mu$ m in B and C, 20  $\mu$ m in D-J.

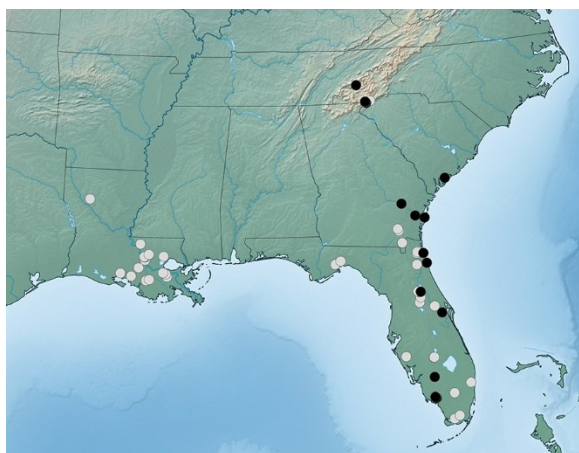


Figure 12. Geographic distribution of *Calopadia puiggarii* in eastern North America based on specimens examined for this study at NY (black) and records from CNALH (gray).