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Between a rock and a hard place: *Chrysothrix susquehannensis* is more widespread in eastern North America than previously thought

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ABSTRACT. – *Chrysothrix susquehannensis* was originally described from vertical rocks faces at a single locality in southeastern Pennsylvania, U.S.A. Here we document new occurrences discovered as result of fieldwork and the revision of herbarium specimens. We show that *C. susquehannensis*, although rare, is widespread in the Appalachian Mountains of eastern North America, with a disjunction in New Mexico in southwestern North America.

KEYWORDS. – Biogeography, cliff ecology, leprose thallus, rare species, rock outcrop, sterile crustose lichen.

INTRODUCTION

Asexually reproducing, typically sterile crustose lichens are poorly understood compared to their fertile counterparts, particularly in terms of biogeographic patterns and ecological requirements (Hodkinson & Lendemer 2012). Even when such species are well delimited and easily recognized, they still suffer from negative collection bias because of the perception that they are difficult to identify (e.g., Lendemer 2020). A likely exception to this phenomenon is the leprose genus *Chrysothrix* Mont. whose members, despite typically being sterile, are frequently collected because of their attractive, highly visible, bright yellow thalli (Elix & Kantvilas 2007, Grube 1998, Laundon 1981).

Chrysothrix susquehannensis Lendemer & Elix was described nearly ten years ago from a single locality on the edge of the Appalachian Mountains in southeastern Pennsylvania, in the northeastern United States (Lendemer & Elix 2010). It is an unusual member of the genus in that it produces gyrophoric acid in addition to rhizocarpic acid, the latter substance gives the species the yellow coloration typical of *Chrysothrix*. Considering the unique chemistry of *C. susquehannesis* — one that is easily detected with standard lichen spot tests — the authors were surprised by the absence of additional collections at the time of its description. Subsequently, while revising specimens on loan for a revision of *Lepraria*, the first author encountered a specimen of the species from western North America. He also identified collections from an inventory of vertical rock habitats in West Virginia conducted by the second author (Clark 2012, Clark & Hessl 2015), who then searched for the species in similar habitats elsewhere. After discovering additional collections from a broad geographic area in the southern United States, we compiled this contribution to provide a more complete account of this rare and interesting species.

MATERIALS AND METHODS

Field surveys. – We conducted extensive field work aimed at locating new sites for *C. susquehannensis*. The first author carried out these surveys in conjunction with broader studies of lichens in North America, spanning more than 1500 individual sites (Figure 1B). At each site where the species was

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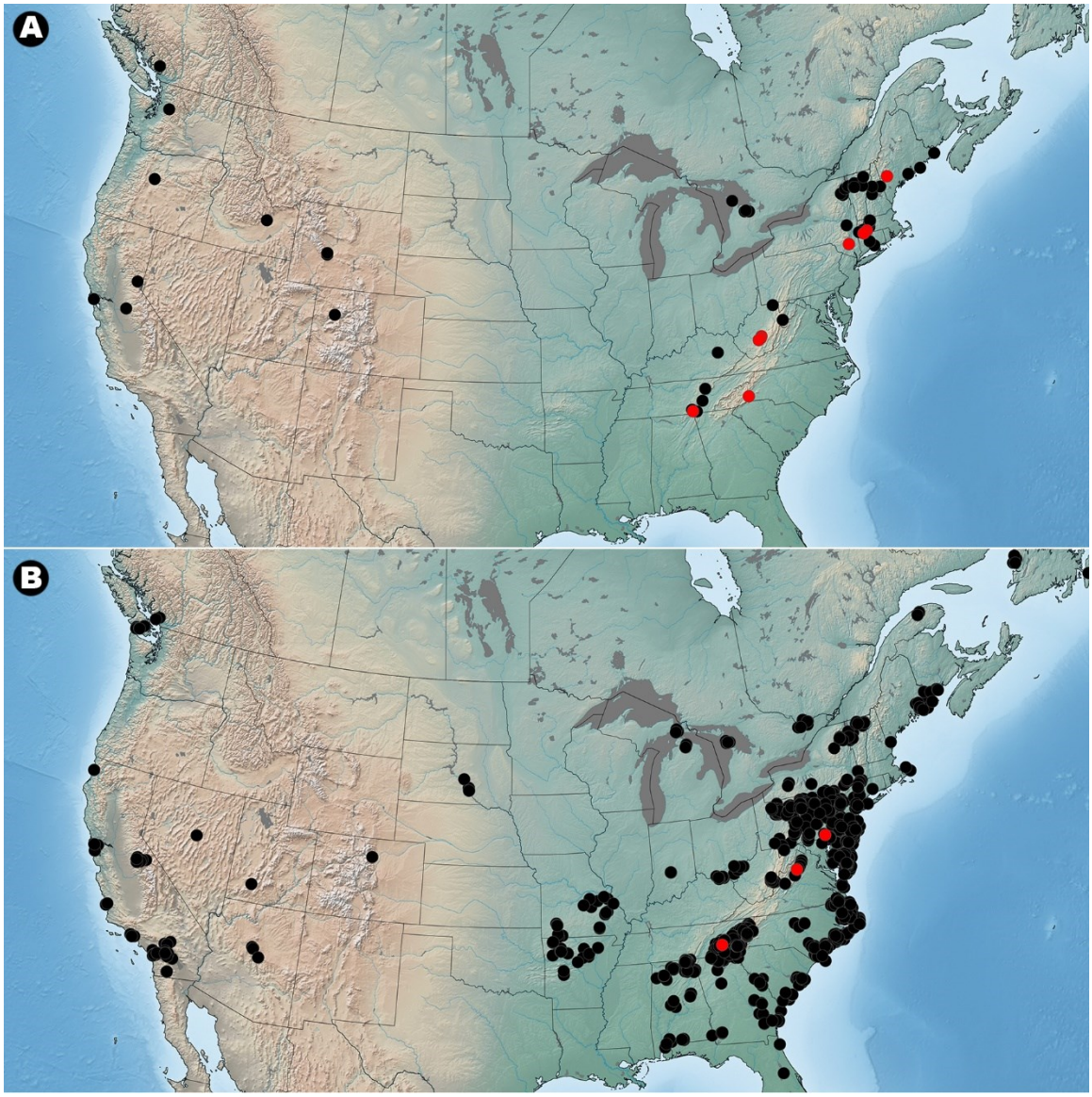

Figure 1, sites studied by the authors (A = Clark; B = Lendemer) where *C. susquehannensis* was not detected (black dots) compared sites where the species was detected (red dots).

detected, a voucher was collected. The second author carried out 61 targeted inventories of lichens inhabiting large cliff escarpments (heights ranging from 10–350 m tall) across the United States and two Canadian provinces (Figure 1A). Cliff sites were examined using technical climbing equipment. A formal evaluation was conducted at a site in West Virginia as part of larger efforts to quantify impacts from recreational activities to cliff-dwelling bryophytes and lichens. The remaining sites were visually assessed by scanning for evidence of *C. susquehannensis* along at least three vertical belt transects (approximately 1.3 m wide) at each site. At these sites, voucher specimens were collected when possible.

Study of voucher specimens. – Specimens examined for this study are deposited primarily in the herbarium of the New York Botanical Garden (NY). Additional specimens were borrowed from the herbarium of the University of Colorado, Boulder (COLO). The morphology of all specimens was studied using a dissecting (Olympus SZ60) and compound microscope (Olympus BH-2). Investigations of the chemistry were conducted with spot tests using standard reagents (Brodo et al. 2001) both directly on fragments of the thallus and on fragments mounted on slides in water. Thin Layer Chromatography was

Figure 2, geographic distribution of *C. susquehannensis* based on specimens examined and fieldwork carried out by the authors.

conducted on selected specimens using solvent C following Culberson and Kristinsson (1970) as modified by Lendemer (2011).

RESULTS AND DISCUSSION

When *C. susquehannensis* was first described, the authors noted that it occurred on massive vertical rock faces that were nearly inaccessible without climbing gear (Lendemer & Elix 2010). They also speculated that the species was likely rare, since it had not been found elsewhere in the region either historically or during extensive modern inventory efforts (see Lendemer & Coyle 2020). The only subsequent published reports have been from the New River Gorge National River in West Virginia (Clark & Hessl 2015) and Great Smoky Mountains National Park in North Carolina (Tripp & Lendemer 2019). Here we report the discovery of fourteen additional occurrences of *C. susquehannensis* from localities throughout the Appalachian Mountains (Maine south to Tennessee) and one location in western North America (New Mexico) (Figure 2). Data for voucher specimens of each occurrence are provided in Appendix I, and data for newly documented sites accessed via climbing are provided in Appendix II. Based on the newly available material, *C. susquehannensis* appears to have a distribution that largely follows other widespread Appalachian leprose lichens such as *Lepraria normandinoides* Lendemer & R.C. Harris and *L. oxybapha* Lendemer (see, Lendemer 2012). While occurrences have not yet been found in the Ozark Highlands or other nearby interior mountainous regions, it is likely the species also occurs there based on the biogeographic patterns of other crustose lichens with similar Appalachian distributions (see Tripp & Lendemer 2019).

Although the known geographic range of *C. susquehannensis* is greatly expanded here, it is important to highlight that the species was found at only a small fraction of the sites that we inventoried for lichens or where we made targeted search efforts for the species (16.4% of 61 sites by Clark; <1% of 1545 sites by Lendemer; Figure 1). Further, across all the sites where the species was detected, the number of individuals varied considerably. For example, in a detailed plot-based study of the New River Gorge National River, West Virginia, numerous individuals (roughly 20 cm^2 in size) were present in 47% of the 552 square meter quadrats that were sampled and *C. susquehannensis* was the seventh most frequently encountered lichen (N=96). At other sites such as Tekoa Mountain, Massachusetts, only a single expansive mat was observed covering several square meters. In many other sites where plot-based ecological data were not collected, the species occurred only as small, spatially isolated colonies.

All the occurrences that we observed in the field, or which have detailed habitat data, were associated with massive rock outcrops, cliff faces or talus slopes (Figures 3A & 4A), often with vertical rock faces that required specialized climbing gear to examine (Figure 4C). Those for which detailed ecological data were collected by the second author were all found on exposed, dry, non-calcareous cliff faces ranging

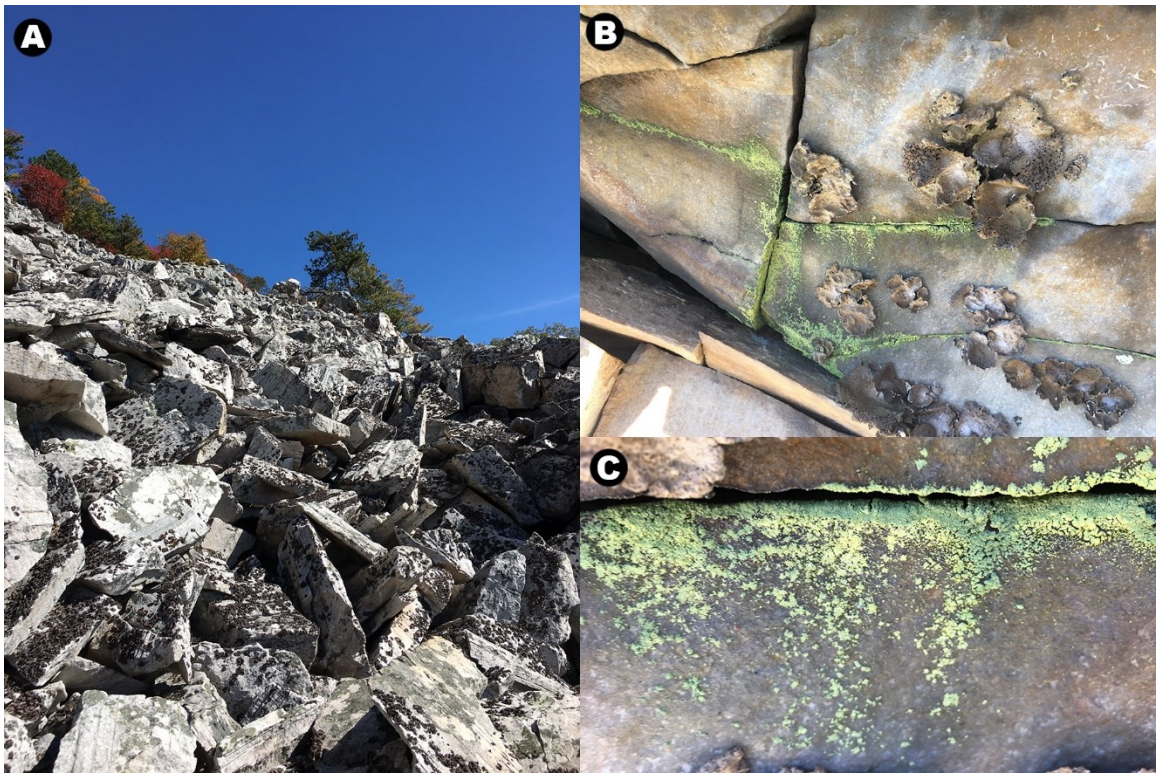

Figure 3, talus slope habitat of *C. susquehannensis* (all photographs by J.C. Lendemer). **A,** large-scale view of a quartzite talus slope in Virginia. **B and C,** appearance of *C. susquehannensis* thalli in the field.

from 25–75 meters tall, with high solar exposure (Clark vouchers in Appendix I; Appendix II). Nearly all occurred high on cliff faces growing at or above tree canopy height, and seldom in lower, more shaded environments, indicating a high degree of shade intolerance.

Chrysothrix susquehannensis habitat appears to be very different from that of *C. insulizans* R.C. Harris & Ladd, a common southern Appalachian cliff associate, which is most frequently found on deeply shaded vertical cliff bases (Clark 2012, Harris & Ladd 2008). Based on our data, *C. susquehannensis* is most prevalent on vertical cliff faces (70–100º from horizontal), occasionally in shallow fissures, but infrequently occurs on ledges or low angle cliffs (<60º from horizontal), on or under overhanging rock (>110º from horizontal), or in deep cracks and seeps (Figures 3B & C, 4B & D). Like many leprose lichens, *C. susquehannensis* is not abundant in environments where there appears to be strong competition from other lichens and was frequently found growing in habitats that did not support large communities of vascular plants or macrolichens (Clark unpublished data; Figure 4D).

Many of the occurrences reported here are from cliffs that have been used for recreational activities such as rock climbing and rappelling for decades. As part of a study in West Virginia, Clark (2012) found no significant differences in the size of *C. susquehannensis* populations between experimental (climbed) and control (unclimbed) sites, suggesting the species may persist under this type of long-term disturbance. Additional anecdotal evidence indicates that under moderate levels of mechanical disturbance from rock climbing, fragile umbilicate and foliose lichens may be reduced while crustose and leprose lichens like *C. susquehannensis* may not be impacted or can even increase in abundance (Boggess et al. 2017, Studlar et al. 2015; Clark unpublished data). These observations indicate some level of adaptability in *C. susquehannensis* to persist or possibly even be enhanced from rock climbing activity.

CONCLUSION

Based on the information presented here, we assert that *C. susquehannensis* is a rare species restricted to a very specific habitat type. Given its propensity to live high on inaccessible vertical cliff faces,

Figure 4, cliff and rock outcrop habitat of *C. susquehannensis* (all photographs by P. W. Clark). **A,** rock outcrop Mount Tekoa in Massachusetts, **B,** typical colony of *C. susquehannensis* at the New River Gorge National River, West Virginia. **C,** vertical cliff at Rumbling Bald, North Carolina. **D,** typical appearance of *C. susquehannensis* (highlighted by arrows) when viewed from a distance, here associated with *Umbilicaria americana* Poelt & T. Nash at the New River Gorge National River, West Virginia.

intensive targeted analyses of suitable habitats are required to develop a detailed understanding of the distribution of, and threats to, this species, as well as a management plan for its critical habitat.

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APPENDIX I – VOUCHERS OF *CHRYSOTHRIX SUSQUEHANNENSIS*

Voucher specimens of *C. susquehannensis* examined for this study are enumerated below. Full data are available from the C.V. Starr Virtual Herbarium at NY (http://sciweb.nybg.org/science2/VirtualHerbarium.asp).

U.S.A. MASSACHUSETTS. HAMPDEN CO.: Tekoa Mountain, Montgomery, above Westfield River and village of Woronoco, 10.xii.2013, on schist, *P. Clark 1510* (NY). **NEW MEXICO.** LUNA CO.: Florida Mountains, 1.6 air miles WNW top of Gym Peak, 12.vii.1991, on rock, *R.D. Worthington 19598* (COLO). **NEW YORK.** ULSTER CO.: Wawarsing-Catskills, Ice Caves Mountain National Landmark, 15.v.1995, on rock, *E. Lay 94-1353* (NY); Shawangunk Mountains, ridge E of Trapps Bridge, vi.2017, on quartz conglomerate, *P. Clark s.n. & A. Tarren* (NY). **NORTH CAROLINA.** RUTHERFORD CO.: Rumbling Bald, Chimney Rock State Park, near Lake Lure, 27.i.2014, on gneiss, *P. Clark 1512 & A. Tarren* (NY). SWAIN CO.: Great Smoky Mountains National Park, Appalachian Trail ca. 0.5 mi S of Shuckstack Fire Tower, 28.x.2016, on rock, *E. Tripp 6065 & J.C. Lendemer* (NY). **PENNSYLVANIA.** LANCASTER CO.: E slopes above Susquehanna River, 0.25–0.5 mi N of confluence of Tucquan Creek and Susquehanna River, 8.viii.2009, on schist, *J.C. Lendemer 19364* (NY!, holotype). **TENNESSEE.** GREENE CO.: Cherokee National Forest, Bald Mountains, Bald Mountain Ridge Scenic Area, S arm of Green Ridge, 9.iii.2018, on rock, *E. Tripp 8487 & J.C. Lendemer* (NY). MARION CO.: Castle Rock, on the northern town limits of Jasper, 23.xii.2013, on sandstone, *P. Clark 1511 & A. Tarren* (NY). **VIRGINIA.** SHENANDOAH CO.: George Washington National Forest, along Signal Knob Trail on Green Mountain, 6.v.2001, on rock, *J. Guccion 2080A-26* (NY). **WEST VIRGINIA.** BRAXTON CO.: Dumpling Run, Mick, Vegetation plot BRAX.1, 19.iii.2013, on rock, *B.P. Streets 4610* (NY). FAYETTE CO.: New River Gorge, site N47Q4, vii.2010, on sandstone, *P. Clark s.n.* (NY); New River Gorge, site N6Q4, vii.2010, on rock, *P. Clark s.n.* (NY). GRANT CO.: Monongahela National Forest, North Rock Mountain, Vegetation Plot MONF.538, 5.ix.2012, on shale, *B.P. Streets 4422* (NY).

APPENDIX II – SITE INFORMATION AND HABITAT DESCRIPTIONS FOR SELECTED NEWLY DOCUMENTED OCCURRENCES

Table 1. Detailed site information (including aspect, cliff height, height of *C. susquehannensis* occurrence, and habitat description) for new studied by the second author.

Site	State	Coordinates	Specimen verification	Aspect	Cliff / population height (ft)	Habitat description
Shagg Crag	ME	44.437596, -70.515270	Field	SE	150 / 50–100	granite and schist, moderate solar exposure, northern hardwood canopy cover to 70 ft, vertical and overhanging cliff
Mount Tekoa	MA	42.166188, -72.812536	Field, lab	S	100 / 30–60	schist, very high solar exposure, no canopy cover, featured cliff with ledges and overhangs
Hanging Mountain	MA	42.072045, -73.066632	Field	SE	120 / 50–110	granite and schist, moderate solar exposure, northern hardwood canopy cover to 70 ft, vertical cliff
Shawangunks Ridge	NY	41.743261, -74.181117	Field, lab	SE	200 / 70–150	Quartz conglomerate sandstone, high solar exposure, oak-hickory-pine canopy cover to 70 ft, vertical cliff with ledges and roofs
Chimney Rock / Rumbling Bald	NC	35.450047, -82.214416	Field, lab	S	80 / 50–80	gneiss, moderate solar exposure, oak-hickory-canopy cover to 50 ft, vertical cliff
Castle Rock Point	TN	35.104070, -85.631260	Field, lab	S	80 / 50–80	sandstone, high solar exposure, oak-hickory-pine canopy cover to 50 ft, vertical cliff