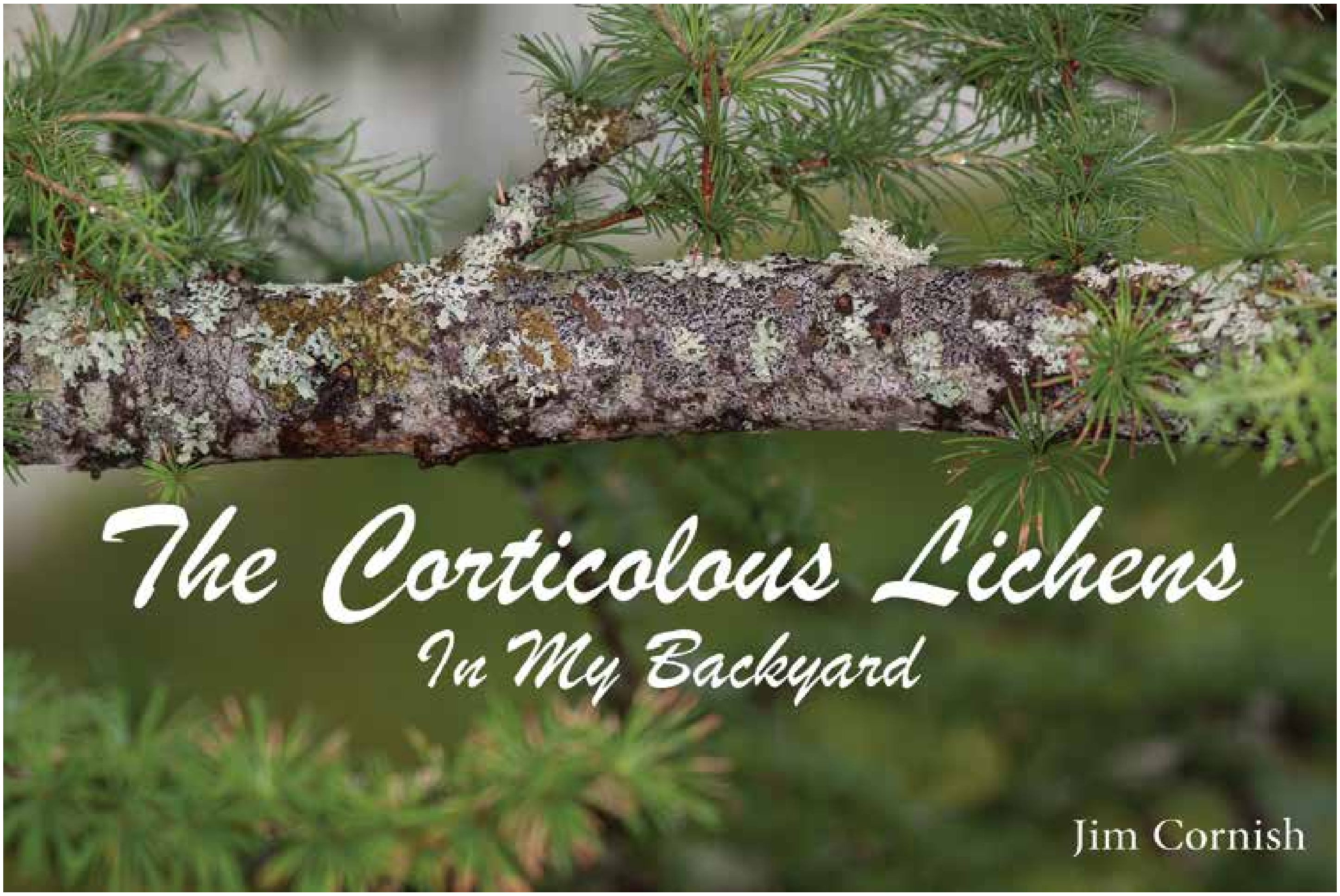

About thirty years ago, my then eight-year-old son and I planted a larch seedling in our backyard. While a seedling, and later as a sapling, the tree survived many brushes with the lawnmower in summer and the deep snowdrifts of a Newfoundland winter. Today at 10 meters tall (33 feet) with a 143-centimeter (56 inch) girth, the tree stands as straight as a schooner's mast. By mid-November, when most other ornamental trees are bare, the larch is the showiest tree in the neighborhood!

During periods of rain, drizzle, or fog, patches of the larch's bark turn a bright grey-green, an unmistakable sign of lichens. When I took a casual look at the trunk, I found a couple of the shield lichen species that commonly grow in boreal forests. But a closer look, this time through a 10X hand lens, revealed much more. On just a 30 cm (12 in) section of a low branch, I discovered a dozen or more corticolous (bark dwelling) lichen species as captured in the banner photo above. What began as an informal examination of the lichens growing in my backyard quickly turned into a macro photoshoot and this article, both of which were great distractions during the Covid-19 pandemic restrictions in Newfoundland and Labrador during the spring and summer of 2020.

What are Lichens?

Lichens are enigmatic lifeforms (Lutzoni and Miadlikowska, 2009)! When the Florentine botanist Pier Antonio Micheli began the systematic study of lichens in 1729, there was little agreement on their true nature or their classification. Carl Linnaeus, the 18th century inventor of binomial nomenclature, was so frustrated by lichens, that he described them as *rustici pauperrimi*, the "poor trash of vegetation," and listed only 80 in his book *Species Plantarum* published in 1753 (Plitt, 1919). In 1869, Swiss botanist and microscopist Simon Schwendener published a paper advancing the radical idea that lichens were not plants as commonly believed at the time, but dual organisms composed of a fungus living with an alga. Schwendener described the relationship as parasitic, akin to a master (the fungus) and his slave (the alga) (Purvis, 2000). Many of Schwendener's contemporaries vigorously and scornfully rejected his proposal, but through the efforts of botanist and mycologist Heinrich Anton de Bary, co-founder of the concept of symbiosis, by the end of the nineteenth century, the lichen duality was widely accepted, and lichens were promoted as a model of a mutualistic lifestyle, i.e., both partners benefit from the relationship (Honegger, 2000; Oulhen, et al., 2016).

Since Schwendener, cyanobacteria have been added as the lone or second photobiotic partner in some 1,500 lichen species (Rikkinen, 2013). More recently, yeast and other fungi and various types of bacteria and other microbes have been identified as additional partners in a growing number of lichens collected worldwide (Spribille et al., 2022). It is believed that these microorganisms may contribute to the health, growth, and fitness of the host lichen (Grimm et al., 2021). Today, the Earth's ~20,000 known lichen species are often called "lichenized fungi" and are considered a consortium of lifeforms from multiple kingdoms living together in a stable and self-sustaining miniature ecosystem (Fashelt, 2008). And while the lichen lifestyle is still considered mutualistic in some respects, how fungi gain nutrition from their photobiotic partners is now regarded as an example of "controlled" or "balanced parasitism" (Nash, 2008).

Lichens are extremophiles and typically endure environments their symbiotic partners are unable to survive independently. Lichens grow in nearly every terrestrial habitat from the equator to the poles and from intertidal zones to 7500-meter (25,000 feet) alpine peaks. Lichens have even survived the vacuum of space and prolonged exposure to unfiltered solar and cosmic radiation in experiments conducted outside the International Space Station and the rigors of Martian atmospheres simulated here on Earth (Brandt et al., 2015). Their symbioses, stratified structure, and ability to dehydrate and suspend all biological activity, enable lichens to survive dormancy for days, and in some cases, hundreds of years. When rehydrated, dormant lichens spring back to life, often unscathed (Lutzoni and Miadlikowska, 2009).

Lichen Structure: The association between a fungus (mycobiont) and its algal and/or cyanobacterial partner (photobionts) gives rise to a thallus, a vegetative body predominately composed of a fungus and unlike any of the partners individually. Multicellular and differentiated, most thalli are stratified into 3 or 4 layers (Fig. 2). The top layer or upper cortex is composed of tightly bound hyphae "cemented" together by polysaccharides and give lichens their structural strength and characteristic shapes. In the absence of pigmentation, the upper cortex of most lichens appears dull greyish green when dry and greener and brighter when wet. The upper cortex is water absorbent during wet periods and slows evaporation during dry spells. Lichen substances (secondary metabolites) produced solely by the mycobiont and stored in crystalline form in the upper cortex act as sun

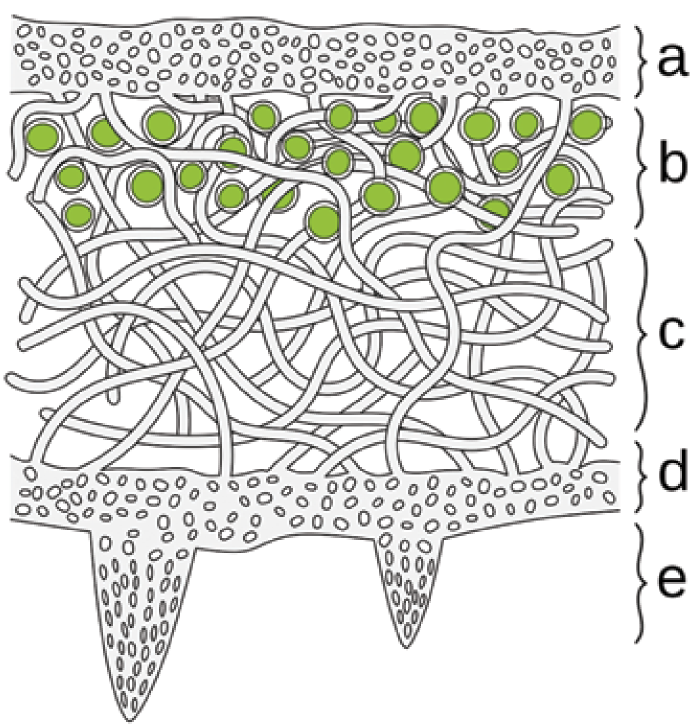

Figure 2. A typical lichen thallus: a: outer cortex; b. photobiont layer with algae and enveloping medullary hyphae; c: medulla; d: lower cortex; e: rhizines. Photo: Wikipedia commons.

Figure 3. *Larix decidua*, the European larch growing in my backyard.

blockers, antioxidants, anti-herbivores, and antipathogens, and protect the algal layer located immediately below. Each photobiont is enveloped by hyphae that originate in the third and thickest thalline layer, the medulla. Composed of loosely arranged hyphae, the medulla creates air spaces for the exchange of O_2 and CO_2 during photosynthesis by the algae. A water repellent layer of protein (a hydrophobin) secreted by the fungus coats the medullary hyphae to keep them dry during wet periods. The protein layer also helps the movement of water and minerals to the photobiont for photosynthesis and the photosynthates the fungus converts to sugar alcohols to all parts of the lichen for growth, maintenance, and reproduction and for protection during periods of dormancy. When present, the fourth layer, or lower cortex, is also composed of tightly woven hyphae and can be bare or covered by hanging, hyphal strands called rhizines that anchor the thalli to the substrate (Brodo et al., 2001; Watkinson et al., 2016).

The Substrate, *Larix decidua:* The tree in my backyard is a *Larix decidua* (Fig. 3), commonly called European larch (Boland, 2013). The tree is native to continental and eastern alpine regions of Europe and was introduced to eastern North America for silviculture research and plantation planting in the mid-1960s (Hall, 1983). Over the years, this species has also been cultivated as an ornamental tree on residential lots and parklands. *Larix decidua* is a fast-growing, monopodial (single trunk) tree that can reach 45 meters (148 feet) in height under optimal growing conditions. The tree's light brown almost greyish bark becomes increasingly scaly and deeply fissured with age. Its branches are slightly upswept while its straw-colored short branchlets typically droop. Often called a "deciduous conifer," the larch's tufted needles look coniferous but like deciduous leaves, they change color and shed in the fall. The tree is also shade-intolerant which makes it an ideal substrate for phototrophic lichens (Boland, 2013).

The Lichens

Crustose Group

Lichens are often grouped based on thalline morphology (crustose, foliose, fruticose, squamulose, and leprose) and type of substratum (rocks, bark, dead wood, and soil). Crustose lichens, the largest of the five morphological groups, are particularly slow-growing, about a 1 mm/year in many cases, and appear as thin crusts on natural substrates and undisturbed manmade objects such as glass, plastic, and rubber, essentially objects on which very little else will grow. Crustose thalli can be continuous, cracked, smooth, or granular in texture and are often the most colorful, sometimes looking more like paint smears than anything alive (Brodo et al., 2001; Watkinson et al., 2016).

Three of the four crustose lichens species found on my larch tree belong to *Lecanora*, a large genus with over 1,000 species distributed worldwide, 170 or more of which grow in North America (Brodo et al., 2003). *Lecanora* often look alike and often require chemical tests and microscopic study of their sexual reproductive structures and spores for identification. The three *Lecanora* described here have distinctively different reproductive structures that will help with identification. In the descriptions that follow, only features easily seen with the naked eye or a 10x hand lens are included. More detailed descriptions for the lichens featured in this article are available from Brodo et al. (2001) and McMullin and Anderson (2014).

Figure 4. *Lecanora circumborealis* (black-eyed rim lichen).

Lecanora circumborealis has a pale grey, thin, patchy, single-layered thallus dotted with sexual reproductive structures called apothecia. Less than a millimeter in diameter, each apothecium has a black to very dark brown disc surrounded by a prominent rim (parathecium) similar in color to the thallus (Fig. 4A). An "individual" thallus is often delineated by a black line called a prothallus (Fig. 4B). *Lecanora circumborealis* is distributed throughout the boreal forests of both North

America and Eurasia and commonly grows above the winter snowpack on both coniferous and deciduous trees. The name *Lecanora* comes from the Greek *lekanon* meaning "a small bowl" and *ora* meaning "beauty." Both are apt descriptions of the lichen's often lightly colored apothecial rim (Brodo et al., 2003; McMillan and Anderson, 2014).

Like other ascomycetes, most lichens produce sexual spores in sacs called asci. These asci are bundled into stalked or sessile globose, cup, or disc-like structures called apothecia. A cup-like apothecium typically contains multiple parts, shown in Fig. 4A: a. the parathecium- the rim composed of upper cortical tissue containing both hyphal and algal cells; b. the epithecium- the tips of sterile asci-supporting hyphae (paraphyses) that give the apothecium its characteristic color and convex, concave, or flat shape; c. the hymenium with spore-bearing asci and sterile hyphae; d. the hypothecium, also composed of sterile hyphae; e. subhypothecium; and f. the medulla.

The rim is typically the same color as the upper cortical hyphae. Lichen apothecia are often perennial features, capable of producing spores for years. In temperate climatic zones, lichen apothecial spore development and dispersal are often timed with the temperatures and relative humidity levels common during the spring and fall. The color, shape, size, and placement of apothecia are all diagnostically important features in species identification (Budel and Scheidegger, 2010; Brodo et al., 2001).

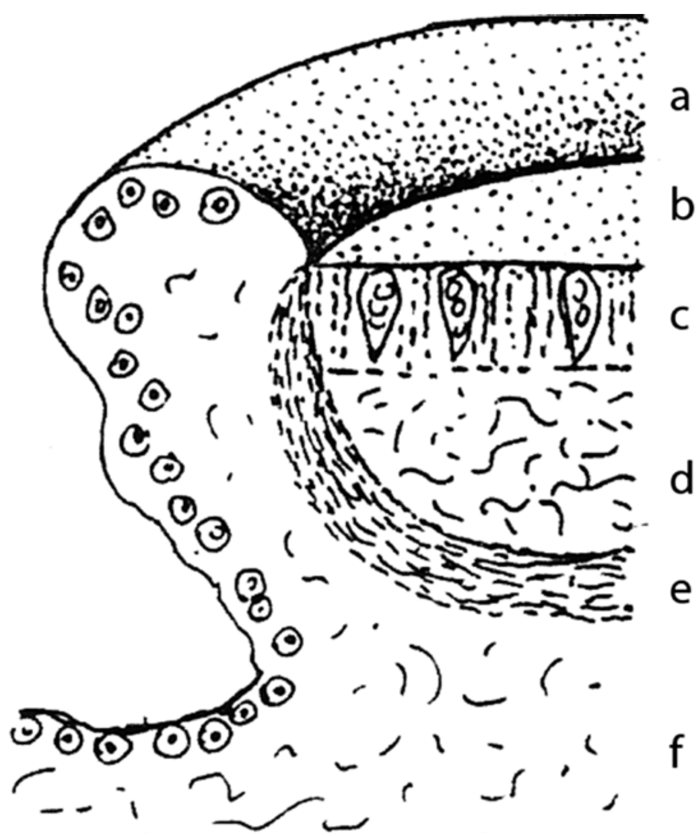

Figure 4A. Lecanorine apothecium.

Figure 4B shows the lichen prothallus. A prothallus forms when thalline fungi grow beyond the lichenized portion of the lichen thallus. Often lacking photobiont cells and either melanized or white, a prothallus forms a fringe that often separates "individual" lichens of the same or different

Figure 4B. Prothallus.

species from one another. A prothallus acts as a barrier, often preventing the same or different crustose species from overtaking one another's space. The presence or absence of a prothallus is also diagnostically important in identifying many crustose species (Brodo et al., 2001; Budel and Scheidegger, 2010). As Fig. 4B shows, *L. circumborealis* has a distinct prothallus that separates it from the adjacent *Buellia disciformis*, another crustose species discussed later in this article.

Figure 5. *Lecanora allophana* (brown-eyed rim lichen).

Lecanora allophana has a somewhat large, thick, white to pale grey, smooth or wrinkled to areolate (cracked) thallus (Fig. 5). The apothecia are lecanorine, often large (up to 2.5 mm in diameter) with distinct, thick, reddish brown pigmented discs and white rims that appear contorted when apothecia are crowded (Fig. 5A). Like many other *Lecanora*

Figure 5A. Crowded apothecia.

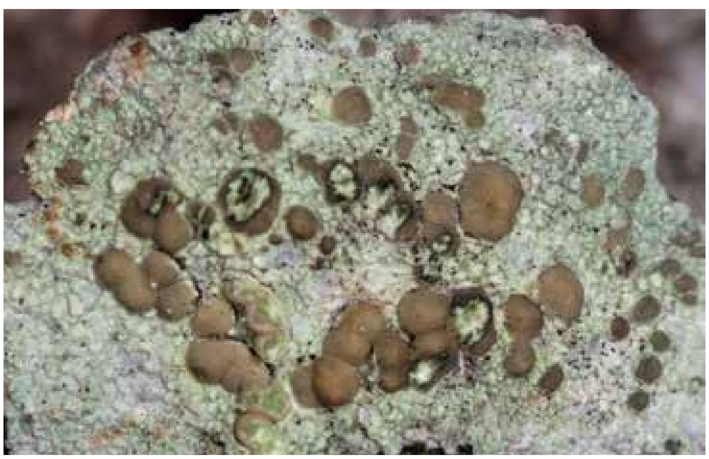

Figure 6. *Lecanora symmicta* (fused rim-lichen).

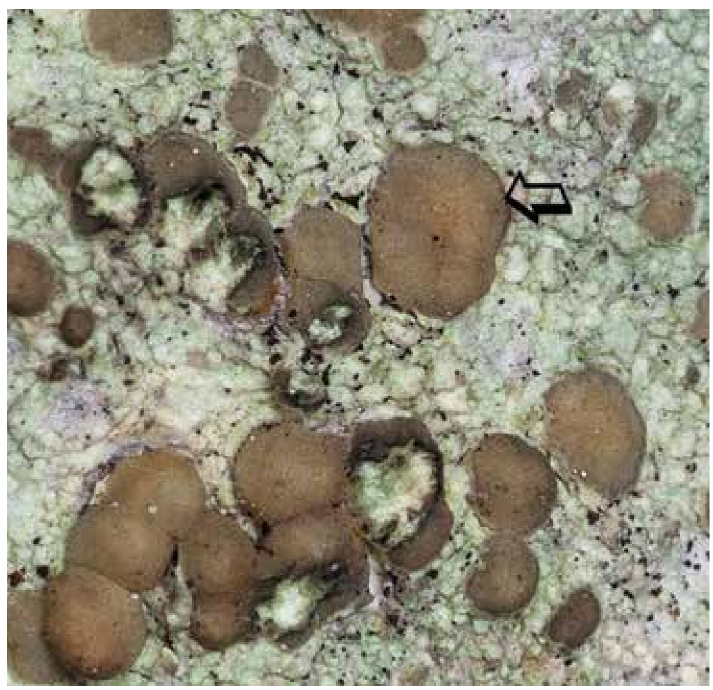

Figure 6A. Fused apothecia: A defining feature of *L. symmicta* is the fusing of crowded apothecia on the thallus.

species, an individual *L. allophana* is separated from other crustose lichens by a robust prothallus. This lichen commonly grows on poplars but also colonizes the bark of other trees and is restricted in distribution to northeastern North America (Brodo et al., 2001). The specific epithet *allophana* means "appearing differently," probably a reference to the apothecia which are larger in this species than in other *Lecanora*.

Depending on the species, lichen apothecia can be spread apart or crowded on a thallus. In *L. allophana*, characteristic crowding often distorts the circular shape of apothecia in this genus. Since *L. allophana* apothecia are relatively large, a hand lens will easily show this distinguishing feature (Brodo et al., 2001).

Lecanora symmicta has a greenish yellow to gray-green or pale green thallus that is often thin and granular. The apothecia are waxy and pale yellowish brown, the latter a result of usnic acid, a pigment that gives many lichens their yellowish color. Usnic acid acts as a UV screen and has antimicrobial

Figure 7. *Buellia disciformis* (boreal button lichen).

Figure 7A. Lichen areoles.

Figure 7B. Lecideine apothecia.

properties that have long interested pharmaceutical researchers (Cocchietto et al., 2002). The lichen's apothecia are less than 1 mm in diameter, flat to slightly swollen and when crowded, often fuse with their neighbors (Fig. 6A). Only young apothecia show a rim. *Lecanora symmicta* grows on coniferous and deciduous tree bark and deadwood and is widely distributed across Canada and the Northeast and Great Lakes region of the USA. The species epithet *symmicta* means "comingled." a reference to its fused apothecia (Brodo et al., 2001).

Buellia disciformis (Fig. 7) has a thin and pale grey to ivory areolate (cracked) thallus (Fig. 7A). Individual lichens are often bounded by a black or grey prothallus. Apothecia are only a millimeter in diameter and appear as raised buttons on the thallus (Fig.7B). The lichen grows on coniferous and deciduous tree bark and is cosmopolitan in distribution. *Buellia* *disciformis* is widespread in the boreal forests of Canada and Europe, and similar trees at higher elevations further south on both continents (Brodo et al., 2001). The genus name *Buellia* acknowledges Esperanzo Buelli, a friend of famous Italian lichenologist and taxonomist Giuseppe De Notaris, who pioneered the use of microscopy in lichen identification. The species epithet *disciformis* refers to the disc-shaped apothecia (Joshi et al., 2010).

Crustose lichen thalli can be cracked (rimose) or extremely cracked (areolate) (Fig. 7A). Areoles form when lower layer hyphae grow faster than the rest of the thallus, forcing it to split into pieces. When surrounded by a prothallus, areoles can make a lichen thallus appear tiled. Often diagnostically important, areoles are easily seen on some rock-dwelling crustose lichens, but a hand lens is often needed to see them on corticolous lichens (Brodo et al., 2001).

One final note on *B. disciformis* lecideine apothecia. The tissue forming the rims of *B. disciformis* apothecia contains hyphae derived from apothecial tissues that lack photobiotic cells. In *B. disciformis*, the perithecium is carbonized, making it appear black and sometimes barely distinguishable from the disc portion of the apothecium, even with a hand lens. (Brodo et al., 2001) (Fig. 7B).

Foliose Group

Foliose lichens have leafy thalli with upper and lower surfaces that usually differ in color and texture. Foliose thalline lobes can be flat or tubular with margins that are rounded or angular and slightly upturned or curled, features that are important in species identification. Most foliose lichens are stratified into 4 layers (Fig. 2). Depending on the genus, foliose lichens have algae or cyanobacteria as photobionts. Some have both. Many foliose lichens are generalists and grow on rocks, soils, and bark and are the most common lichen group found on trees. Corticolous foliose thalli are often loosely attached to the bark substrate by rhizines or by a single holdfast of cortical hyphae that penetrates the surface and grows among the cells of the cork layer. Some foliose lichens are subfruticose and rise above the substrate (Brodo, 1973). At least seven species of foliose lichens were found growing on the larch in my backyard.

Vulpicida pinastri has a bright to dull yellow upper cortex and a dull yellow to white lower cortex that is often covered in rhizines. Thallus lobes are 1–2 cm (0.4–0.8 in) wide with upturned margins that are a brighter yellow than the rest of the thallus and trimmed with vegetative reproductive structures called soredia (Fig. 8A). The lichen grows on conifers, often within a meter or two of the ground, possibly using the snowpack as protection from harsh winter weather. It is one of a growing number of lichen species threatened by climate change and habitat loss. *Vulpicida pinastri* has been studied for its vulpinic, pinastric, and usnic acids, all ultraviolet blocking secondary metabolites. It is distributed across temperate regions in the northern hemisphere. The genus name *Vulpicida* means "fox killer," a reference to the toxicity of its vulpinic acid to wolves. The specific epithet *pinastri* refers to its growth on Pinaceae, the pine family of trees (Brodo et al., 2001; McMullin and Anderson, 2014).

Many lichens reproduce asexually via vegetative structures called soredia. Unique to lichens, soredia are powdery or granular bundles of algal cells enveloped by hyphae, essentially making them lichens without a cortex (Fig. 9A). Soredia appear on ruptures called soralia that form along lobe margins and along ridges on the upper cortex. Soredia are water repellent and are actively discharged and dispersed by chance, often by the force of wind and falling raindrops or by contact with passing insects, birds, and animals. Heavier than spores, soredia are less likely to be dispersed great distances, at least by the wind. Soredia have an advantage over ascospores

Figure 8. *Vulpicida pinastri* (powdery sunshine lichens).

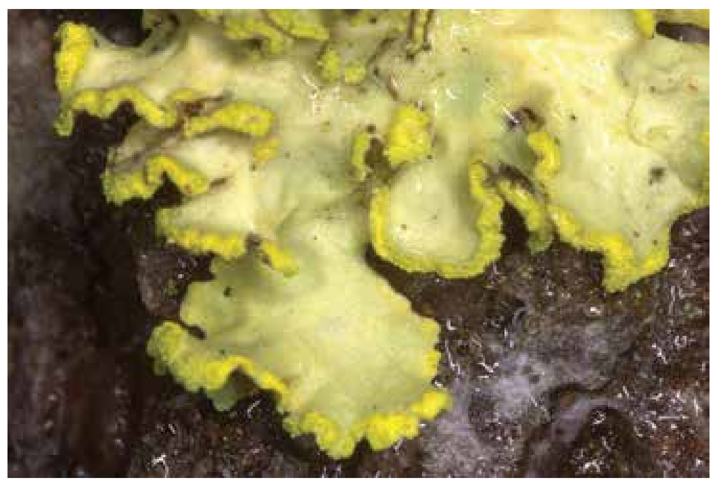

Figure 8A. *Vulpicida pinastri* soredia.

Figure 9. *Parmelia sulcata* (hammered shield lichen).

Figure 9A. Soredia.

Figure 9B. Rhizines.

Figure 10. *Melanohalea septentrionalis* (northern brown shield).

in synthesizing new lichens. Although both symbionts are dispersed together the alga and fungus must separate and then relichenize (come back together) to synthesize a new lichen. Spores, on the other hand, often contain only mycobiont cells and their germ tubes must find a compatible photobiont partner before a lichen can form, a requirement that is thought to have a lesser chance of succeeding (Jahns, 1973; Pyatt, 1973).

Parmelia sulcata (Fig. 9) has a grey-green, radial, and branching lobed thallus that is partially attached to the substrate by bottlebrush-like black rhizines (Fig. 9B). The upper cortex is covered in a distinct network of white ridges that gives it a furrowed or hammered-metal look. *Parmelia sulcata* reproduces mainly via soredia which on older specimens occurs on cracked ridges and/or on lobe margins. Apothecia are rare on this species. The lichen grows on well-lit coniferous and deciduous trees, on rocks, and on undisturbed wooden surfaces. Often considered "weedy," the lichen is distributed throughout all of Canada and in the northern parts of the USA. It is also widespread in temperate and sub-boreal regions in the Southern Hemisphere. The genus name Parmelia means "shield-like" while the specific epithet sulcata means furrowed (Brodo et al., 2001; McMullin and Anderson, 2014). When growing on the narrow branches and branchlets, the lichen is often elongated and far less shield-like in appearance.

Rhizines are linear, multi-cellular root-like bundles of hyphae that grow from the lower cortex of many foliose lichens. Typically using a disk-like holdfast, rhizines clasp substrate particles such as mineral grains in rocks and cork cells in the bark to anchor its lichen host in place. Often melanized, rhizines come in many shapes (branched, unbranched, forked, straight, or tomentose) and often vary in their density over the lower cortical surface. While rhizines may hold water, unlike roots they have no vascular mechanism to transport it or any nutrients to the thallus. Foliose lichens lacking rhizines typically use a single central peg or holdfast to affix them to the substrate. Rhizines are diagnostically important in species identification and details of their shapes are more easily identifiable under a compound microscope (Brodo et al., 2001; Jahns, 1973).

Melanohalea septentrionalis has a small, smooth to slightly wrinkled (matted) and appressed thallus often varying in shades of olive-green on the upper cortex and dark brown underneath. The broad and flat apothecia are abundantly clustered in the center of the thallus. The lichen lacks soredia and other asexual reproductive structures. The lower cortex is covered with brown unbranched rhizines (Fig. 10). *Melanohalea septentrionalis* grows on a variety of coniferous and deciduous trees. It is distributed through the boreal forest of North America and Eurasia. The genus name *Melanohalea* refers to the dark brown to melanin-rich thallus (*melano*) and the American lichenologist Mason Hale, Jr (*halea*). The specific epithet *septentrionalis*, meaning "northern regions," referring to its boreal distribution (Brodo et al., 2001; McMullin and Anderson, 2014).

The genus *Hypogymnia* contains most of the tube-like arboreal lichens common in boreal forests (Fig. 11). The lichen has a thallus of branching flattened tubes about 1–5 mm in width and variable in length. These tubes are smooth and pale greenish gray, often turning pale brown on any upturned and inflated lobe tips. Tube margins may be covered in soredia. The lower surface is wrinkled and typically brown at the margins and black towards the center. *Hypogymnia physodes* has a circumpolar distribution across boreal and temperate forests in the northern hemisphere. Preferring acidic bark, the lichen grows abundantly on coniferous trees but can also be found on deciduous ones. Because of its sensitivity to sulfur dioxide and heavy metals, *H. physodes* is often used as a bioindicator of air quality. The genus name *Hypogymnia* means "naked," a reference to its lack of rhizines on the lower cortex. The specific epithet *physodes* means "tubes" (Brodo et al., 2001; Molnar and Farkas, 2011).

Figure 11. *Hypogymnia physodes* (hooded tube lichen).

Figure 12. *Xanthoria polycarpa* (pin-cushion sunburst lichen).

Xanthoria polycarpa has a bright yellow-orange to orange pigmented thallus that appears as small irregular-shaped cushions (2.5 mm in diameter) on the substrate (Fig. 12). The thalline lobes are narrow, abundantly branched, and irregular. Apothecia are abundant, dark orange with bright orange rims, that are often contorted when crowded in the center of the thallus. *Xanthoria polycarpa* grows on nutrient-rich bark, twigs, branches, wood, and rocks. The lichen's presence is an indication of nitrogen-rich substrates commonly associated with bird excrement, so they often form large colonies along coastlines. Distribution is scattered but common in Atlantic West Coast (British Columbia and USA). The genus name *Xanthoria* refers to the pigmented secondary metabolite that gives the lichen its yellow color. The specific epithet *polycarpa* means "many fruits," referring to its many apothecia (Brodo et al., 2001; McMullin and Anderson, 2014).

Lichenization: Trees provide ideal environments for the wind dispersal of spores from apothecia-rich lichens like *M. septentrionalis*. With few exceptions, spores contain no photobiotic cells, so they must land and germinate in the vicinity of a compatible photobiotic partner and join (lichenize) before a lichen can form. Fortunately for many lichen-forming fungi, a variety of algae can be a suitable partner. Once

Figure 13. *Physcia aipolia* (hoary rosette lichen).

Figure 13A: Maculae.

lichenized, the fungus can choose a new partner if a more compatible one becomes available or swap partners with another lichen. It can also steal a more suitable partner from an adjacent lichen (Piercey-Normore, 2006).

Biomonitors: Lichen are sensitive to air pollution because they have no way to regulate or rid themselves of airborne chemicals. Pollutants like sulfur dioxide and heavy metals tend to accumulate in lichens and affect thallus size, apothecial development, and overall survival. Consequently, the form and presence or absence of lichens are bioindicators of air quality. Individual lichens and whole lichen communities are often used to biomonitor the changing health of the environment and to evaluate the rate of recovery of areas where air pollution has been reduced or its sources eliminated (Walewski, 2007; Purvis, 2000). The presence of *Bryoria*, *Hypogymnia*, and *Ramalina* is an indication of good air quality.

Lichen Pigmentation: Many lichens lack pigments and appear as shades of green or grey-green when dry, then greener when wet. The rest are colorful because some of the secondary metabolites deposited in the upper cortex are pigments. Yellowish colors come from usnic acid and pulvinic acids and xanthones. Bright yellow, orange, and red colors come from anthraquinones. Browns and blacks come from melanin. The brightest lichens often grow in areas of greatest direct exposure to sunlight. Intraspecific changes in coloration are common because pigment concentrations can change depending on thallus age, exposure to sunlight, genetics, and variable environmental factors (Brodo et al., 2001).

Figure 14. *Platismatia glauca* (ragbag lichen).

Physcia aipolia has a pale to dark grey thallus with narrow radiating lobes and upturned tips (Fig. 13). The thallus is conspicuously spotted with white maculae (singular: macula) (Fig. 13A). The lower surface is white to pale brown and thickly covered in rhizines. Cilia may be present on lobe margins. The apothecia have black discs with grey rims, are up to 3 mm in diameter, and are typically scattered over the thallus. Sometimes apothecia are covered in a fine "frosting" called pruina, not present in Fig. 13, maybe because the lichen has not yet matured. The lichen grows on many tree types and dead wood in open habitats and is widely distributed across North America. The genus name *Physcia* means "inflated" and refers to the appearance of its lobes. The specific epithet *aipolia* means "hoary" and refers to its pruinose apothecia. Its look-alike, *Physcia stellaris*, has about the same range, but has flat or somewhat convex lobes that lack maculae (Brodo et al., 2001).

In some lichens, the photobiont layer is not always continuous. Since it contributes to the overall color of the thallus, areas free of photobionts will show as paler spots or lines called maculae on the upper cortex (Brodo et al., 2001). Maculae textures resemble painting textures done by dabbing a sponge.

The thallus of *Platismatia glauca* is more erect on the substrate than most foliose lichens and is considered an intermediary species. The lichen has a ruffled and ragged-looking thallus with wide, leafy, floppy lobes often pale green to white on top but reticulated (interlaced lines) and pale brown below. In older specimens, the margins are often divided into small rounded or angular brown lobes with isidia or soredia occurring abundantly, usually on different specimens. In the image (Fig.14), isidia are beginning to appear on the margins of some lobes. Apothecia are rare and rhizines are scarce. *Platismatia glauca* grows on spruce and fir and is commonly found in the eastern section of Canada's boreal forest and the mountain ranges of southern British Columbia and Alberta. The genus name *Platismatia* means "broad-lobed" while the specific epithet *glauca* means "pale grey," a reference to the color of its upper cortex (Brodo et al., 2001; McMullin and Anderson, 2014).

In some foliose lichens, the lower cortex may appear wrinkled or ridged (Fig. 14A). Called reticulations, these ridges are caused by the bundling of cortical hyphae. Lower cortical reticulation is characteristic of *P. glauca*, although it might

Figure 14A. Reticulation.

Figure 15: *Tuckermannopsis orbata* (variable wrinkle-lichen).

appear different from specimen to specimen.

Tuckermannopsis orbata has a variable olive-brown to pale green thallus that typically darkens in color when exposed to sunlight (Fig. 15). The subfruticose thallus has wrinkled and irregular-shaped lobes with black finger-like projections called isidia (Fig. 15A) and black hairs called cilia (Fig. 15B) along its margins. Apothecia are common, flat, brownish, and usually develop near the lobe margins on both the upper and lower cortical layers. The lichen grows on conifers and occasionally hardwoods but is limited to northeastern North America, British Columbia, and the upper westernmost of the USA. The genus is named after lichenologist Edward Tucker, while the specific epithet *orbata* refers to its circular apothecia (McMullin and Anderson, 2014).

Like soredia, isidia are unique to lichens. They appear as minute, finger-like outgrowths, usually on crustose, foliose, and fruticose lichen thalli. Isidia contain both lichen partners and a cortical layer. Because isidia increase the surface area of the lichen thallus, they likely contribute to the photosynthetic output of the whole lichen. Brittle when dry, isidia are easily detached and dispersed by wind and/or animal vectors. Once they find a suitable habitat, isidia can grow into new lichen thalli (Jahns, 2010; Purvis, 2000).

Cilia are algae-free eyelash-like extensions of hyphae from the lobe margins or apothecia of certain lichen thalli. Black or white, they often vary in length and branching. Cilia might play a role in anchoring a lichen to its substrate, but their real purpose is not known. Like many thallus features, cilia are diagnostically

Figure 15A. Isidia.

Figure 16. *Evernia mesomorpha* (boreal oakmoss lichen).

Figure 15B. Cilia.

Figure 16A. *Evernia mesomorpha* soredia.

significant in species identification (Brodo et al., 2001).

Pycnidia are the flask-shaped asexual reproductive structures that bear conidia, i.e. asexual spores or male sex cells. Pycnidia are black and stand out conspicuously above the thallus. In some species, they are embedded in the thallus and are far less visible. The conidia are released through an opening (ostiole) in the pycnidia and can germinate just like ascospores, giving this lichen an extra chance at reproducing. (Brodo et al., 2001).

Fruticose Group

Fruticose lichens are shrub- and hair-like in appearance and are believed to be the last lichen form to evolve. Missing a lower cortex, the three remaining layers are arranged concentrically to form cylindrical or flattened tubular stems (podetia) that grow singly or in tufts on soils, trees, and rocks (Purvis, 2000). Some podetia are hollow while others are filled with medullary hyphae. Fruticose lichens grow erect and keep their shape via long thick-walled cortical cells. Some hair-like fruticose species hang like tresses from trees and have an elastic central cord for mechanical strength. Most fruticose lichens are attached directly to the substrate via a holdfast. Some hair-like varieties are simply draped over their tree branch substrates (Brodo et al., 2001). Three fruticose species from three separate genera were found growing on the lower trunk and branches of my larch tree.

Evernia mesomorpha thalli are composed of pale yellow-green tufts with divided, angular, wrinkled, and uneven branches 4–8 cm (1.5–3 in) long and around 3 mm wide. Branch margins are typically covered in coarse soredia (Fig 16A). The lichen grows on the trunks and branches of both coniferous and deciduous trees. The lichen has a circumboreal distribution and is common throughout most of boreal North America and the continent's north-central plains (Brodo et al., 2001; McMullin and Anderson, 2014). The lichen is pollution tolerant, being one of the first species to recover after pollution damage (Piercey-Normore, 2006). The genus name *Evernia* means "many branches" while *mesomorpha* refers to its ridged branches (McMullin and Anderson, 2014).

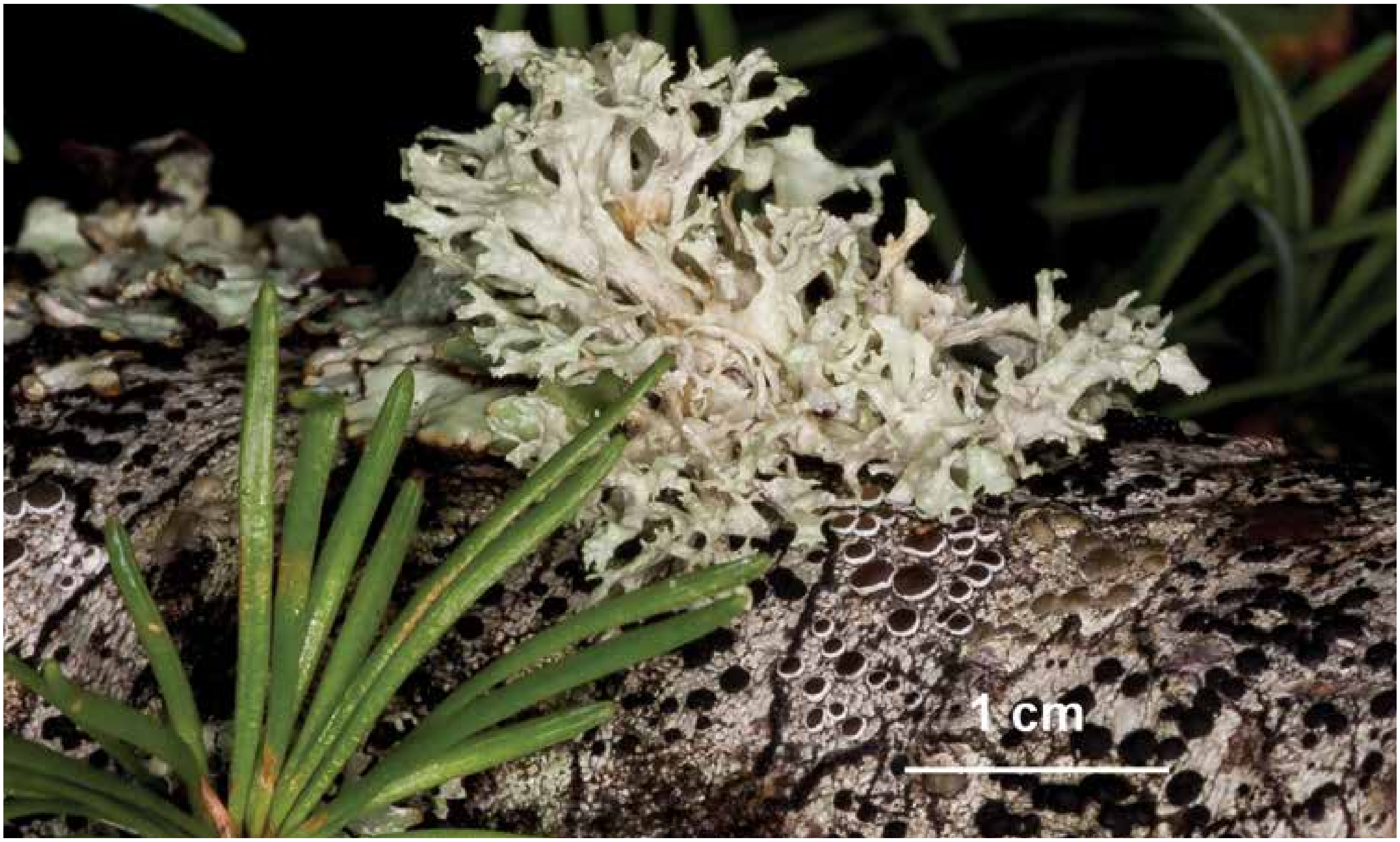

Figure 17. *Ramalina dilacerata* (punctured ramalina).

Figure 18. *Bryoria trichodes* (horsehair lichen).

Figure 18A. Pseudocyphellae.

Figure 19. The species diversity on this 15-centimeter section of the lowest larch tree branch contains over half of the lichens found.

Lichens that lack apothecia often use soredia as the main means of reproduction. Apothecia are rare on *E. mesomorpha*, so the lichen's branch ridges are abundantly covered in coarse soredia (Piercey-Normore, 2006), something that is best seen under magnification.

Ramalina dilacerata has a pale greenish yellow, thin, flat, smooth, and hollow thallus. The lichen appears as dense, and highly branched tufts and grows on coniferous tree trunks and branches. Immature specimens often lack the apothecia that form on the branch tips, so young *R. dilacerata* can easily be mistaken for some *Usnea* and *Alectoria* species. *Ramalina dilacerata* is limited in distribution to most of Atlantic Canada, New England, the Great Lakes region, and the northern coastal mountain ranges of western North America. The genus name *Ramalina* means "twigs" while the specific epithet *dilacerata* means "twice torn," a reference to its perforated branches (Brodo et al., 2001; McMullin and Anderson, 2014).

Epiphytes: Corticolous lichens are epiphytes, organisms that grow on other organisms but gain their nutrition from the surrounding environment. Epiphytes must attach themselves to their host's bark by extending their rhizines into the cork layer. *Evernia mesomorpha* and *Ramalina dilacerata* and other fruticose lichens typically use a single or relatively few points of attachment called holdfasts which are formed of basal hyphae that extend deeper into the bark than rhizines, in some cases going all the way to the cambium layer. These attachments do not remove nutrients from their hosts and do not directly harm the tree. However, some research suggests that holdfasts may open the inner bark to infectious microbes that can lead to tree health problems (Brodo et al., 2001).

Bryoria trichodes is the only living hair lichen represented on the larch tree. A species, likely a *Usnea*, was too young and possibly dead and could not be positively identified. *Bryoria trichodes* has a dull, pale to dark brown pendant thallus that can hang up to 15 cm (6 in) from the substrate. It is held in place by a single holdfast or simply draped over a branchlet, suggesting it originated elsewhere and was snared by the branch. Apothecia and soredia are uncommon and are scattered over the thallus when present. Whitish pseudocyphellae (Fig. 18A) are short, oval, and tend to bend the branches. The lichen often grows on the twigs and branches of conifers, particularly near rivers, lakes, and marshlands. The lichen is widely distributed in northeastern North America from the Great Lakes to Newfoundland. *Bryoria* is a combination of two older names of this group of hair lichens, *Bryopogon* and *Alectoria*, and *trichodes* meaning "hairy" (Brodo et al., 2001; McMullin and Anderson, 2014).

If there is an inadequate exchange of gases in specific regions on the thallus, a lichen's upper cortex can break down to form 0.1 to 2 mm diameter pores that can help restore the equilibrium between gas exchange and the metabolic needs of the lichen. Called pseudocyphellae, these pores can be filled by ascending medullary hyphae and often appear as white spots on the upper cortex (Zanetti et al., 2017).

Corticolous Lichen Ecology

Propagule Capture and Dispersal: Lichen spores, soredia, and isidia are collectively called propagules. They lack the wings, parachutes, and burrs that aid dispersal, yet they take advantage of the same vectors as plants to spread their "seeds." The larch in my backyard is in the open and exposed to the wind. Its rough bark can easily snag locally, and regionally sourced propagules from the passing air. Once established, the new lichen colonists likely spread locally, taking advantage of these same winds to dislodge new propagules and spread the species to other surfaces of the tree (Brodo, 1973; Armstrong and Bradwell, 2010).

Many birds and squirrels visit the larch tree in my backyard (Figs. 20, 21). Lichen propagules were likely dispersed from local and/or regional lichen populations by these animals who often use the larch as a perch and as a source of insect food and nest-building materials. These animals are also known to trample dry brittle lichens, fragmenting their thalli, and dislodging propagules that can get caught in their feet, fur, and feathers. Such propagules are later deposited where the animals perch and preen. The presence of *Xanthoria*, a genus commonly associated with nitrogen-rich bird excrement, is an indication of the role birds play in lichen dispersal (Bailey and James, 1979; Brodo et al., 2001).

Corticolous Lichen Succession and Substrate Specificity: One of the oldest challenges in ecology is understanding the co-existence of species and explaining their community composition (Prieto et al., 2017). Of the hundreds of arboreal lichens identified in Newfoundland, why these fourteen species were selected at the exclusion of others can be explained by a variety of factors including the specificity of the resident lichens, and the age of the tree, and the characteristics of larch bark as a living substrate (Brodo, 1973).

All fourteen lichens did not arrive and colonize the tree at the same time. Studies on corticolous lichen succession suggest that generalists, i.e., widely distributed species capable of growing on a variety of substrates, were likely the first lichen to become established. These generalists include the circumboreal and faster-growing *H. physodes*, and *P. sulcata* that dominate the tree, particularly the trunk. Fruticose species follow, leaving crustose lichens like *Lecanora* as the climax species (Brodo et al., 2001).

Corticolous lichen diversity and species richness can be influenced by factors including the age of the tree, its bark characteristics of texture, stability, chemistry, acidity (pH), and moisture retention, and environmental factors such as light availability, air quality, temperature, and humidity levels.

Planted thirty years ago, the larch had plenty of time to become colonized by lichens. As a sapling, the tree's widely spaced branches, scattered needle whorls, and sparse branchlets left plenty of bark exposed to rainwater and sunlight, which created the alternating wet-dry cycles lichens prefer for growth. Over the years, wind-dispersed propagules snagged by the tree's exposed and rough bark likely gave rise to the first lichens. Resins in the bark's cork layer likely make the substrate acidic which undoubtedly favored some lichen species while excluding others. The scaly and porous outer bark also enabled the tree to absorb and retain water directly from rainfall. The resulting stem flow and slow evaporation likely created humid microenvironments that provided enough moisture to extend the lichens' growth periods for days after a good rain. For organisms that grow slowly and only when moistened, even a few days of growth can help ensure survival. Moisture transpired through cracks in the bark and dissolutions of sap and gum residues that trickled down the branches and trunk may have favored some species over others (Brodo, 1973; Sillet et al., 2000; MacDonald et al., 2017; Király et al., 2013).

Figure 20-21. Courtesy D. Brophy.

Conclusions

We plant trees in our backyards to beautify our property, to celebrate the birth of a child, to pay tribute to a departed family member, to enjoy the shade it provides on a sunny day, or to provide shelter against winter winds. With time, that tree will likely have many roles: a holdfast for a hammock, support for a swing, and a center beam for a treehouse. Ecologically, the tree will likely serve many more roles. As the larch on my property demonstrates, backyard trees, and the ones planted in community parks, provide important habitats in degraded urban landscapes and suburban sprawl stripped of its trees for housing. Planted trees also have the potential to preserve biodiversity by providing a refuge for species across many Kingdoms as they help to bridge gaps in ecosystems fragmented by our towns and cities. While that seems so obvious now, it is something I had not considered when I planted the larch many years ago.

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