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Plant and Fungal Systematics 64(2): 117–135, 2019
DOI: 10.2478/pfs-2019-0014

ISSN 2544-7459 (print)
ISSN 2657-5000 (online)

James Donald ('Jim') Lawrey: a tribute to a unique career in lichenology

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The year 1949: James D. Lawrey's birth year put in context

The year 1949 was an important year. Shortly after the end of the disastrous World War II, the world began to reshape at a global level. In April of that year, the North Atlantic Treaty Organization (NATO) was founded, including several countries of Western Europe, the United States, and Canada. Just one month later, the Federal Republic of Germany came into existence, and in September, the People's Republic of China was proclaimed. Perhaps even more impacting were the sociocultural novelties introduced during that year. In August of 1949, the Basketball Association of America (BAA) merged with the National Basketball League (NBL) to form the brand name of the National Basketball Association (NBA). In June of the same year, Gertrude Augusta 'Gussy' Moran shocked Wimbledon by wearing a miniskirt on the court. Much to the delight of the first author of this tribute, in that year also the so-called 'currywurst' was invented in Germany, credited to a woman named Herta Heuwer, who owned a food stand in Berlin. Jim hadn't been born yet to witness these events, but would learn about them eventually in history classes or through documentaries. Whether he has ever tasted a traditional 'currywurst' is not known.

The year 1949 also saw major advancements in science. Albert II, a rhesus monkey, was the first mammal to reach space alive (Beischer & Fregly 1961). Willard Libby and his team from the University of Chicago invented the radiocarbon dating technique (Arnold & Libby 1949), for which Libby received the Nobel Prize in 1960. John B. S. Haldane, who twenty years earlier had introduced the 'primordial soup theory' as a hypothesis for abiogenesis, proposed the 'darwin' as unit of evolutionary change: a generation-based, proportional and logarithmically transformed morphometric measure (Haldane 1949). Famous people with 1949 as their birth year include actors Sigourney Weaver (famous for 'Alien' and portraying Dian Fossey in 'Gorillas in the Mist'), and Brent Spiner ('Data'); musicians Gloria Gaynor and Bruce Springsteen; Elisabeth Ann Warren, first female Senator from Massachusetts and Democratic hopeful for the 2020 elections in the United States. Precisely on December 15, 1949, Don Johnson was born. Who doesn't remember Miami Vice? And, of course, our outstanding 'Jim', the subject of this tribute.

The year 1949 also marked a recovery in the number of papers published in the field of lichenology after the war, as evidenced by the Recent Literature on Lichens (RLL) database (Timdal 2010). Pre-war levels of around 200 papers per year from the early 1930s to around 1940 had dropped to less than 100 towards the end of the war and its immediate aftermath (1943–1946), with a steady increase between 1947 and 1950 to reach again pre-war numbers (Fig. 1). Among the authors publishing in 1949 were Henry des Abbayes (France), Harry H. Allan (New Zealand), Yasuhiko Asahina (Japan), Maurice Bouly de Lesdain (France), Maurice Choisy (France), Gunnar Degelius (Sweden), Ivan Mackenzie Lamb/Elke Mackenzie (Great Britain, Argentina), A. Hugo Magnusson (Sweden), W. Fritz Mattick (Germany), Alfred N. Oxner (Ukraine), Veli Räsänen (Finland), Rolf Santesson (Sweden), John W. Thomson (USA), and Ruggero Tomaselli (Italy), to name a few. Allan (1949) published the first modern key to Peltigeraceae subfamily Lobarioideae ('Stictaceae') of New Zealand, recognizing the genera *Lobaria* and *Sticta*, the latter at the time also including *Pseudocyphellaria*. Thomson (1949) followed up on his treatments of Wisconsin lichens with a revision of Teloschistaceae (*Teloschistes* and *Xanthoria*). After return from his travel to South America, Santesson (1949) published two new genera from Chile, *Dolichocarpus* and *Xanthopeltis*, a presumably minor contribution, but one of the groundbreaking papers of this author that would challenge established views on lichen taxonomy and systematics. Mackenzie Lamb, who was working in Argentina at the time, published a study on lichen biogeography

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in the Southern Hemisphere (Lamb 1949). The post-war era saw an increasing interest in antibiotic properties of lichen substances (e.g. Shibata & Miura 1949). The same year also marked the beginning of the debate about the status of lichen fungi and their nomenclature. Diehl (1949) noticed that Art. 64 of the *Cambridge Rules* (Briquet 1935) would render names applied to lichens illegitimate (‘*nomina confusa*’), and proposed that lichens be treated as fungi, a provision that was subsequently integrated into the *Stockholm Code* (Lanjouw et al. 1952).

Enter the picture: James D. Lawrey, plant and fungal ecologist

In 1949, our newborn Jim likely had no idea that only about a quarter of a century later he himself would enter the field of lichenology early into his doctoral dissertation work, with a paper on heavy metal accumulation in *Cladonia* lichens growing in an abandoned coal strip-mining area in Ohio (Lawrey & Rudolph 1975). Two years earlier, Jim had completed his master’s dissertation on floodplain plant community ecology in South Dakota and Nebraska (Lawrey 1973). He would further deepen his skills as a plant and fungal ecologist during his doctoral dissertation work, focusing on trace metal cycling in complex plant and fungal communities in an abandoned coal strip-mining area in Ohio (Lawrey 1977a). Notably, his advisor, the late Prof. Dr. Emanuel D. (‘Rudy’) Rudolph (who passed away in 1992; Stuckey 1994), had been working on the taxonomy and ecology of Antarctic and North American lichens since the 1950s (Cooper & Rudolph 1953; Rudolph 1953, 1955, 1965, 1966; Dodge & Rudolph 1955; Anderson & Rudolph 1956; Showman & Rudolph 1971; Williams & Rudolph 1974). Yet, lichens played only a peripheral role in Jim’s Ph.D. dissertation, which resulted in no less than eight rather swift publications, two focusing on lichens (Lawrey & Rudolph 1975; Lawrey 1977b) and one on cryptogams including lichens (Lawrey 1978a), chiefly *Cladonia*. The other, main papers dealt with plant and fungal communities (Lawrey 1977c–e, 1978b, 1979).

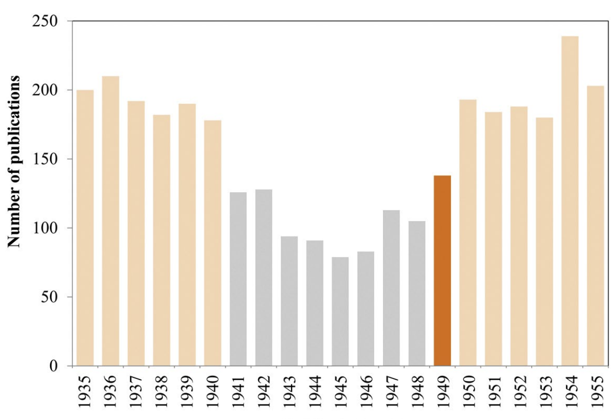

Figure 1. Number of publications on lichens registered in the Recent Literature on Lichens (RLL) database (Timdal 2010) between 1935 and 1955, highlighting the development after World War II and in Jim’s birth year, 1949.

However, already during his dissertation work, Jim had commenced some lichen-related side projects that would determine his scientific interests for the next two decades. He published a first paper on lichen-invertebrate interactions with Robert D. Slocum, discussing the role of epizoic lichen communities for dispersal and camouflage (Slocum & Lawrey 1976). Slocum was working on his master’s dissertation on the effects of SO_2 and pH on *Trebouxia* photobionts at the time; coincidentally, while he would later specialize in plant biochemistry, Slocum published two further lichen papers, on the structural aspects of the lichen symbiosis in *Dictyonema* basidiolichens (Slocum & Floyd 1977; Slocum 1980), a subject Jim would become deeply involved with thirty years later.

During his dissertation work, in 1976, Jim met the late Mason E. Hale Jr., who invited him to participate in long-term lichen growth studies that had commenced on Plummers Island in the Potomac River, Maryland (Fig. 2). Plummers Island, part of the U.S. National Park Service, is considered ‘…*the most thoroughly studied island in North America*…’ (Fig. 2A). Studies there began already in 1899 in conjunction with the foundation of the Washington Biologists’ Field Club (WBFC; Krombein 1963). In 1939, WBFC members Emery Leonard and Ellsworth Killip published the first larger survey of lichens of Plummers Island (Leonard & Killip 1939). Mason Hale had established long-term lichen plots on the island in 1959 and was elected to membership in the WBFC in 1961. He published the first of several lichen growth studies about a decade later (Hale 1970). His work on Plummers Island and with the WBFC was honored with a plaque (Fig. 2D).

Jim’s encounter with Mason, Plummers Island and the WBFC would define his future research for three decades to come. In 1982, Jim himself would be elected a member in the WBFC, later serving as vice president 1993–1996 and as president 1996–1999. Notably, the WBFC, whose members dedicate themselves to the ‘… *biological sciences and particularly … the promotion of research upon the fauna and flora of the District of Columbia area*…’, was until 1996 only open to male members, although female researchers could historically obtain funds from the club for scientific projects.

Plummers Island lichen monitoring plots: breeding ground for long-term environmental pollution and ecological studies

Immediately after obtaining his Ph.D. in 1977, Jim was appointed Assistant Professor at George Mason University in Fairfax, Virginia, in close proximity to Washington and the Smithsonian, which fostered his close collaboration with Mason Hale and the work on Plummers Island. Their first joint publication appeared in the same year, analyzing growth rates of selected foliose and crustose lichens based on long-term photographic documentation (Lawrey & Hale 1977). The authors reported annual radial growth rates of approximately 3–5 mm/year for foliose macrolichens in the family Parmeliaceae, including *Punctelia* (as *Parmelia*) *rudecta*, *Flavoparmelia* (as *Pseudoparmelia*) *baltimorensis*, and *Xanthoparmelia conspersa*. In contrast,

Figure 2. Plummers Island and Mason Hale: James Lawrey's early work relations. A – Plaque with background of the site. B – Mason Hale with his setup for long-term photographic documentation of lichen growth. C – Mason Hale with Jim Bennett. D – Plaque in honor of Mason Hale's work on Plummers Island. E – Location of Plummers Island. F–G – The younger Jim was instrumental in working with Mason Hale to analyze and publish important results from the long-term plots on Plummers Island. Photographs by Manuela Dal Forno (A, D), James Lawrey (B, C), Matt Perry (F, G), and Google Maps (E).

crustose microlichens such as *Graphis scripta* and *Protoparmeliopsis* (as *Lecanora*) *muralis* exhibited rates of less than 1 mm/year. This appears to have been the first study to systematically use photographic documentation (Fig. 2B) for a broad array of species during a period of several years.

At the end of 1962, the American Legion Memorial Bridge (at the time named Cabin John Bridge) had been opened to traffic, an interstate highway bridge crossing the Potomac River and situated immediately west of Plummer Island (Fig. 2E). The much increased pollution through automobile exhausts offered an opportunity to study long-term pollution impact on the lichen communities of Plummers Island, compared to other long-term plots on the nearby but much less affected Bear Island. Jim and Mason correlated substantially increased lead accumulation in lichens on Plummers Island over a period of four years (1974–1978) with decreased growth rates in young lichen thalli of *Flavoparmelia baltimorensis* (Fig. 3), a study published in *Science* (Lawrey & Hale 1979). In a subsequent paper, comparing historic and recently collected samples of three species from various localities in northeastern North America, Jim and Mason showed a dramatic increase of lead accumulation in lichen thalli especially through the 1970s (Lawrey & Hale 1981). Focusing on *Flavoparmelia baltimorensis*, the same authors demonstrated that lead accumulation followed a saturation pattern, reaching a plateau in thallus portions at least two to three years old (Lawrey & Hale 1985). In a later study on the same taxon in Shenandoah National Park in Virginia, Lawrey & Hale (1988) found that increased sulfur and decreased lead concentrations correlated with temporal patterns of these pollutants in the area.

Jim's early academic years can be considered a textbook career. Obtaining a master's degree at the age of 24, a doctoral degree by age 28, and an immediate appointment as Assistant Professor of Biology at George Mason University, with a *Science* paper as lead author at the age of 30, are extraordinary achievements any student would dream of. Yet, during the early years at George Mason University, the logistics to establish a research lab were difficult for faculty positions, who in turn had a rather heavy teaching load. But naturally, Jim made his best efforts to continue part of his research at the Smithsonian with Mason Hale. Apart from the pollution monitoring and ecological studies stemming from long-term plots on Plummers Island and at other sites, one rather unique paper emerging from this collaboration was an analysis of reproductive strategies in the genus *Parmotrema* (Fig. 4), a group Hale had worked on extensively (Hale 1965, 1974). Analyzing a large number of species, with data Mason had amassed over the years, Jim was able to demonstrate significant differences in the distribution of reproductive strategies in temperate vs. tropical species (Lawrey 1980a). He interpreted these results as an adaptation of temperate species to a more unpredictable environment, with species propagating by vegetative propagules frequently also producing ascospores for *de novo* lichenization, thus more flexible in their reproductive strategies.

With his broad interest in ecology, Jim also expanded the focus of the long-term plots on Plummers Island and Bear Island to look into aspects of lichen community ecology and interspecific competition. Comparing a saxicolous community on the pollution-affected Plummers Island with that of a less-affected community on Bear Island, he found that higher pollution levels led to lower species richness. This in turn caused a niche shift in one of the dominant species, *Xanthoparmelia conspersa*, due to competitive release, because of the absence of important competitors in the pollution-affected community (Lawrey 1981). Through the following decade, Jim and Mason continued to work on various long-term plots, with field work mostly supported by the Washington Biologists' Field Club, but Mason's unexpected death in 1990 from cancer prevented him from seeing most of the fruits of this hard work published. Shortly after Mason's passing, Jim published three further papers in memory of Mason Hale, based on long-term observations of these lichen plots: two on community assembly focusing on species-area curves (Lawrey 1991a, 1992) and one with an extended analysis of various pollutants affecting lichen communities (Lawrey 1993a). Apart from these more scientifically oriented studies, Jim continued working on long-term lichen pollution monitoring in protected areas and for the National Park Service during an extended period until recently (Lawrey 1993b, 2011).

Jim concluded the community ecology aspect of his scientific work with an elegant theoretical-empirical review on lichen community development processes involving competitive exclusion (Lawrey 1991b), thereby testing four hypotheses: (1) strong competitors replace weak competitors; (2) specialists replace generalists; (3) chemically well-defended species replace poorly-defended species; (4) long-lived species replace ephemeral ones. He presented evidence that the degree competitive exclusion correlated with community life span, being highest in short-lived foliicolous and lowest in long-lived saxicolous communities. Some indication but no strong evidence was found for niche specialists, chemically complex lichens, and long-lived species being more competitive. Jim pointed out the difficulties to clearly measure these parameters and test them experimentally, setting the stage for future studies, including his own to follow on the ecological roles of lichen secondary compounds.

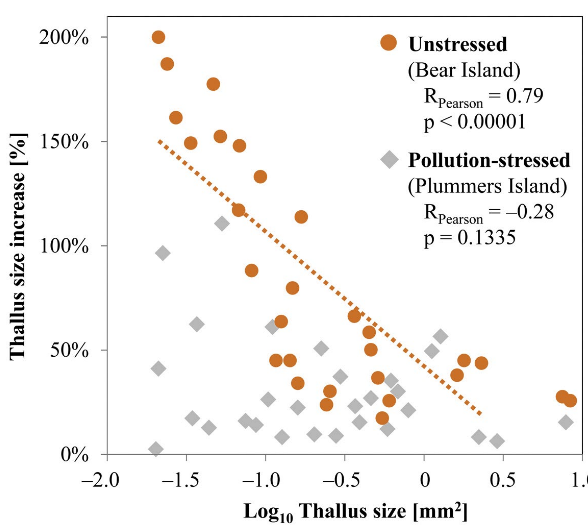

Figure 3. Effect of automobile exhaust pollution on relative annual thallus increase in thalli of different sizes (ages) of *Flavoparmelia baltimorensis*, in a pollution-stressed (Plummers Island) vs. a non-stressed site (Bear Island). Graph adapted after Lawrey & Hale (1979: fig. 1). Instead of the natural logarithm, we used log_{10} and recalculated Pearson's R for both sites. Following the original graph, the regression line for the unstressed Bear Island site is indicated.

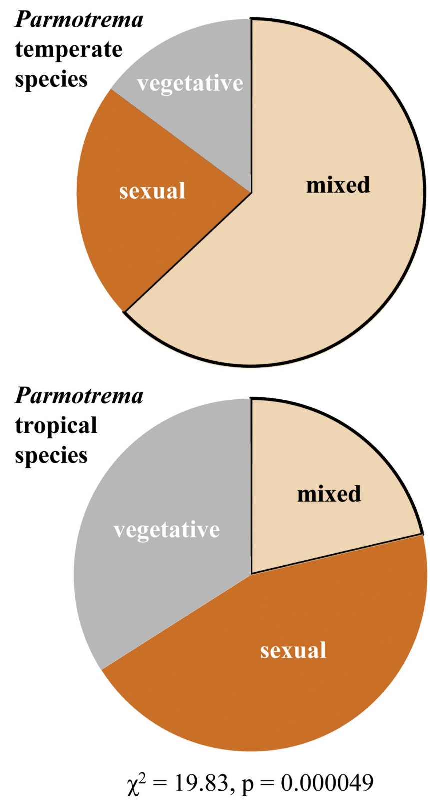

Figure 4. Difference of the proportion of exclusively sexually vs. vegetatively reproducing vs. mixed species in temperate vs. tropical species of *Parmotrema*. Graph adapted from Lawrey (1980a: table 1) and statistics recalculated using a non-parametric Chi-Square test.

Fortunately, due to pioneers such as James Lawrey, the field of modern, hypothesis-driven lichen ecology has maintained strength despite the increasing popularity of molecular phylogenetic studies: in the time span from 1970 to 1995, prior to the beginning of the molecular era, and precisely covering Jim's contributions to the field, the RLL database (Timdal 2010) lists 868 papers under the keyword 'ecology' and just 33 under 'phylogeny'. During the subsequent period of practically equal length (1996–2019), even more papers on 'ecology' were published (951), although studies on 'phylogeny' increased nearly 20-fold (640).

Lichen-invertebrate interactions and chemical ecology of lichens

While finishing his doctoral thesis, and perhaps also inspired by Mason Hale's work on lichen chemistry, Jim became interested in the potential ecological roles of secondary lichen compounds. He initially studied the allelopathic effects of various substances produced by *Cladonia* and other species on germination of spores of co-occurring mosses (Lawrey 1977f, g). Following this research, he obtained an NSF grant (DEB-7824367) on *The Chemical Ecology of Lichens*. As a result of this project, he published two studies on calcium accumulation in lichens and subsequent uptake by herbivores, and general correlations between lichen secondary chemistry and grazing activity by lichenivores (Lawrey 1980b, c).

Expanding on this successful project, Jim obtained another grant from the NSF (DEB-8100354), for a project entitled *Lichen-Invertebrate Chemical Interactions*. During this project, Jim and a master's student advised by him, John Whiton, expanded on the possible allelopathic function of lichen compounds (Whiton & Lawrey 1982, 1984). Jim also found that different lichen acids affected grazing activity by the slug *Pallifera varia* differently and that lichen preference by this species was better explained by levels of chemical deterrents than by nutrient quality (Lawrey 1983a, b). In one of these lichens, *Vulpicida* (as *Tuckermanopsis*) *pinastri*, concentrations of the compounds usnic, vulpinic and pinastric acid correlated with thallus size and age rather than with environmental factors (Golojuch & Lawrey 1988), which the authors also interpreted as evidence for a potential role of lichen acids in deterring lichenivores. Jim summarized these and other findings in two review papers, an assessment on the biological role of lichen substances (Lawrey 1986a), which has been cited well over 300 times, and a summary of interactions between invertebrates and their licheny and mossy substrates (Lawrey 1987). In a follow-up study, Jim found a correlation between the function of secondary compounds as antilichenivore defense and antimicrobial activity (Lawrey 1989).

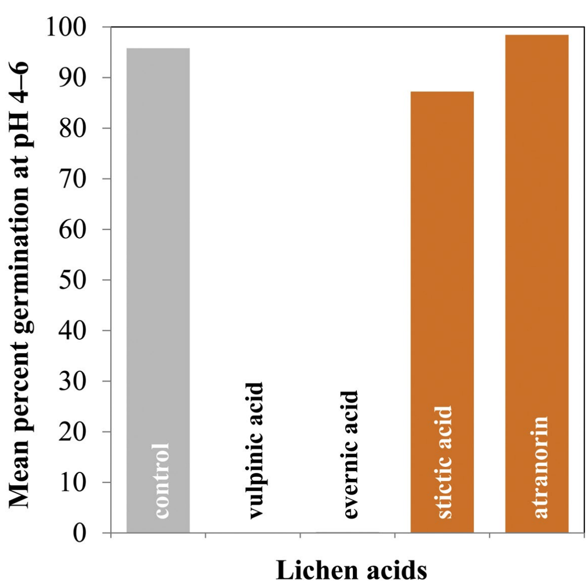

Figure 5. Experimental inhibition of ascospore germination in the lichen fungus *Graphis scripta* by selected lichen acids. Graph adapted from Whiton & Lawrey (1984: table 1). Ascospore germination is barely inhibited by stictic acid and atranorin but strongly so by vulpinic and evernic acid.

The allelopathic effects of lichen substances, a topic summarized in another review by Jim (Lawrey 1995a), had been the subject of previous studies (e.g. Burzlaff 1950; Harder & Uebelmesser 1958; Barbalic 1963; Follmann & Nakagava 1963; Miller et al. 1963; Brown & Mikola 1974; Rundel 1978). However, Jim's meticulous experimental approaches raised some interesting questions. First, in order to actually function as allelopathic substances, lichen compounds would have to be released onto the surrounding substrate, which is counterintuitive given that lichen acids are hardly water-soluble. Also, detected effects, such as the inhibition of ascospore germination in *Graphis scripta* by vulpinic and evernic acid (Fig. 5), do not necessarily reflect natural scenarios. *Graphis scripta* is a shade-tolerant lichen mostly growing on smooth-barked trunks, whereas lichens containing vulpinic acid, such as *Letharia vulpina* and *Vulpicida pinastri*, thrive in sun-exposed habitats and often on branches and twigs. Very rarely do these lichens occur together, which means that experimentally observed allelopathic effects may not be relevant in nature. Given these limitations, lichenicolous fungi attacking lichen thalli promised to be a much better model system to analyze such effects. We do not know whether this was indeed Jim's line of thought, but perhaps this is why he came to focus on the biological relationships between lichenicolous fungi and their host lichens, a subject that became the center of his research and where he has made his most important scientific contributions.

Chemical ecology of lichenicolous fungi

Jim's first study on the potential correlations between lichenicolous fungi and lichen metabolites brought him back to the long-term monitoring sites at Bear Island (Lawrey 1993c). Jim had observed that the lichenicolous fungus, *Illosporiopsis* (as *Hobsonia*) *christiansenii* (later reidentified as *Marchandiomyces corallinus*; see Torzilli et al. 1999), almost exclusively attacked a single lichen, the saxicolous *Flavoparmelia baltimorensis*, and to a much lesser extent the closely related, corticolous *F. caperata*. The established plots allowed Jim to analyze the frequency of the lichenicolous fungus quantitatively in the field, resulting in an occurrence of about 5% of the sampling plots. Under laboratory conditions, the fungus grew on dried tissues of *F. baltimorensis* and *Xanthoparmelia conspersa*, but not on *Lasallia pustulosa*, *Myelochroa aurulenta*, and *Punctelia rudecta*, except when secondary substances had previously been removed through acetone wash. On filter paper containing acetone extracts of the species, the fungus grew best with extracts of *F. baltimorensis*. These results were perplexing as there were no clearcut chemical differences that would explain the observed differences between *F. baltimorensis* and the other four lichens: three of the five substances found in *F. baltimorensis* (usnic acid, atranorin, gyrophoric acid) were in part also found in each of the other four lichens, and apart from these, the chemistry of the other four lichens was non-overlapping. Jim therefore concluded that a specific combination of substances was not only responsible for the observed preferences of the lichenicolous fungus but actually stimulated its growth and degradative behavior (Lawrey 1997).

Jim and his collaborators further explored the potential role of lichen compounds on lichenicolous fungi with a broader array of species, including *Ovicuculispora* (as *Nectria*) *parmeliae* and *Pronectria oligospora*, members of the Hypocreales, on the same host lichens, with similar results compared to *I. christiansenii* a.k.a. *Marchandiomyces corallinus* (Lawrey et al. 1994). They also found that the inhibiting effect of certain lichen metabolites was not restricted to growth of the lichenicolous fungus but also extended to the function of cell wall-degrading enzymes produced by the latter (Torzilli & Lawrey 1995). These and results of other studies were summarized in a review (Lawrey 1995b). Further studies showed that another lichen pathogen in the Hypocreales, belonging to the genus *Fusarium*, was well-adapted to degrading lichen fungal tissue by overcoming the chemical defense of the host lichen (Lawrey et al. 1999; Torzilli et al. 2002).

Perhaps the most elegant of Jim's work is that involving the lichenicolous fungi *Marchandiomyces corallinus* (Fig. 6), *Ovicuculispora parmeliae*, and *Fusarium* sp. on the host lichens *Flavoparmelia baltimorensis*, *Lasallia papulosa*, and *Punctelia* (as *Parmelia*) *rudecta*. Jim's team found that, under laboratory conditions, *M. corallinus* grew well on the host lichen *F. baltimorensis* but was inhibited by *L. papulosa*, presumably because of the different underlying host chemistry (Torzilli et al. 1999). Yet in the field the fungus occasionally also attacked *Lasallia pustulata*. Through laboratory experiments (Fig. 7), the team found that this only occurred when the host lichen had already been attacked by a particular *Fusarium* species that degraded the apparently inhibitory substance lecanoric acid (Lawrey et al. 1999). The same *Fusarium* also facilitated growth of the parasite *Ovicuculispora parmeliae* on the otherwise avoided host lichen *Punctelia rudecta*, again with lecanoric acid as main medullary compound (Lawrey 2000). The apparently undescribed lichenicolous *Fusarium* species (with the culture number NRRL 26803) belongs in the *F. larvarum* complex, which is the anamorph of the biocontrol agent *Nectria aurantiicola* (Bills et al. 2009). This close relationship highlights lichenicolous fungi as model systems to study

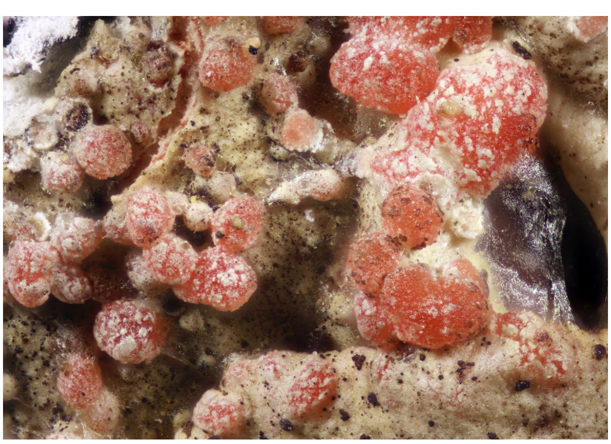

Figure 6. The lichenicolous fungus *Marchandiomyces corallinus*. Photograph by Paul Diederich.

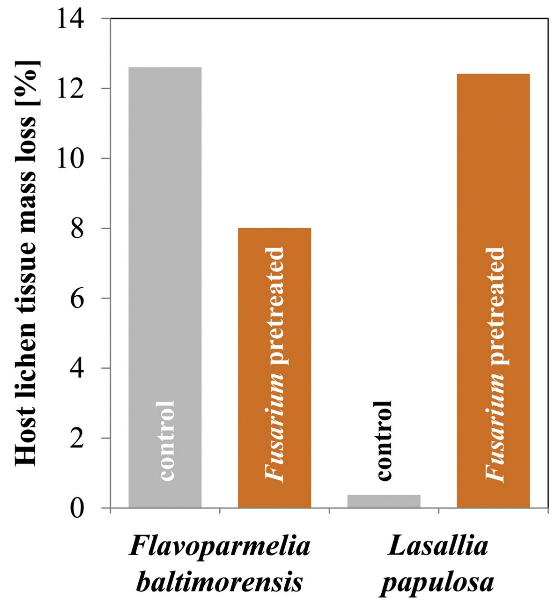

Figure 7. Enhanced growth of the lichenicolous fungus *Marchandiomyces corallinus* on the otherwise avoided host lichen *Lasallia papulosa* after previous degradation by a specific strain of *Fusarium* (NRRL 26803); growth on the usually preferred host lichen *Flavoparmelia baltimorensis* under the same laboratory conditions for comparison. Graph adapted from Lawrey et al. (1999: fig. 3).

and explore chemical interactions in parasite-host associations, a field in which Jim has set standards for experimental approaches and establishing model organisms (Lawrey 2002). In the case of the *Fusarium* facilitating the growth of both the basidiomycete *Marchandiomyces corallinus* and the ascomycete *Ovicuculispora parmeliae*, it is notable that the *Fusarium* is related to *Ovicuculispora* but not at all to *Marchandiomyces*. This offers interesting perspectives on the role of phylogenetic relationships in such complex interactions.

Possibly because of this line of thought, in the past two decades Jim focused on evolutionary relationships of lichenicolous fungi and evolution of the lichenicolous lifestyle in fungi (Lawrey & Diederich 2003). Yet, he would take up the general subject of lichen chemical defenses, including against UV radiation, lichenivores, microorganisms, and lichenicolous fungi, in another, very detailed review (Lawrey 2009). Notably, to that point his pioneering studies on the chemical biology of lichen-lichenicolous fungus interactions would remain unique, and only recently Jim's elegant experimental approaches seem to have been taken up again (Merinero et al. 2015; Asplund et al. 2016; Merinero & Gauslaa 2017).

Phylogenetic relationships of lichenicolous fungi and evolution of the lichenicolous lifestyle: emergence of new, successful collaborations

Jim's interest in lichenicolous fungi has continued to the present day, with a shift towards evolutionary questions after the turn of the millennium (Sikaroodi et al. 2001). This also marked the beginning of a very successful and long-term collaboration with Paul Diederich and Damien

Ertz (Lawrey & Diederich 2003; Lawrey et al. 2007; Diederich et al. 2018), although Jim had known Paul already since the IAL3 in Salzburg 1996. Jim, Paul and Damien and their collaborators have provided numerous important contributions on the evolution of lichenicolous Basidiomycota and Ascomycota and the diversity of lifestyles in these phyla (DePriest et al. 2005; Molina et al. 2005; Diederich & Lawrey 2007; Lawrey et al. 2007, 2008, 2011, 2012, 2015, 2016; Diederich et al. 2011, 2012, 2013, 2014, 2018; Ertz et al. 2014, 2015; Suija et al. 2015).

The first phylogenetic paper on lichenicolous fungi co-authored by Jim, on three of the species studied by him in earlier works, namely *Illosporiopsis* (as *Hobsonia*) *christiansenii*, *Hobsonia santessonii*, and *Marchandiomyces corallinus* (Sikaroodi et al. 2001), somewhat cryptically offered an interesting story of perplexing convergence between ascomycetous and basidiomycetous lichenicolous lineages. Prior to Jim's work on *Illosporiopsis* (as *Hobsonia*) *christiansenii*, Lowen et al. (1986), when describing the fungus for the first time, found that it agreed with *Marchandiomyces corallinus* in all aspects, including pigment chemistry, except for the nature of the conidia, and the authors hypothesized that the two taxa could represent different stages of the same species. Jim therefore had adopted the name *Illosporiopsis* (as *Hobsonia*) *christiansenii* for what later turned out to be *Marchandiomyces corallinus* (see above), and the phylogenetic analysis demonstrated that the two fungi belonged to different phyla. This example suggests that entirely unrelated fungal lineages may evolve similar functional traits when developing into highly adapted lichenicolous pathogens. Notably, this phenomenon would emerge again in Jim's subsequent involvement in the study of basidiolichen evolution.

In 2010, Lawrey & Diederich established the first online checklist of lichenicolous fungi (Lawrey & Diederich 2010). This marked Jim as an expert in lichenicolous lineages and brought him invitations to participate in various recent, multi-authored systematic and nomenclatural papers (Hyde et al. 2013; Hibbett et al. 2014; Wijayawardene et al. 2014; Rossman et al. 2015). The highly useful checklist of lichenicolous fungi was recently published as an exhaustive printed reference (Diederich et al. 2018), which has already been cited over 20 times in a single year.

Jim and basidiolichens: the *Dicytonema* story

Given Jim's work on lichenicolous Basidiomycota, and particularly the recognition of the presumed basidiolichen genus *Marchandiomphalina* (Diederich & Lawrey 2007), it seemed natural that he would expand his interest to basidiolichens in general. Besides his collaboration in a study on *Lepidostroma* (Ertz et al. 2008), a first occasion to dive deeper into the topic was Jim's participation as instructor in the first OTS lichen course in Costa Rica in 2007, organized by Robert Lücking, Jim, José Luis Chaves and Bibiana Moncada. The diversity of basidiolichens at the course locality, Wilson Botanical Garden and Las Cruces Biological Station, was striking, including *Cyphellostereum* and *Lepidostroma* and filamentous and foliose forms then known as *Dictyonema*. The idea ripened to investigate the phylogenetic placement of these lichen-forming fungi. Two years later, Jim and his team published the first broad-scale phylogeny of *Dictyonema* and related basidiolichens, with the surprising find that *Dicytonema* s.lat., *Cyphellostereum*, and *Acantholichen* formed a monophyletic group closely related to *Lichenomphalia* in the *Hygrophoraceae* (Lawrey et al. 2009). In parallel, the team investigated the question whether filamentous and chroococcoid cyanobacterial photobionts in filamentous vs. foliose *Dictyonema* species represented different genera, as presumed at the time (*Scytonema* vs. *Chroococcus*) or modifications of the same photobiont. The even more surprising result was that the two photobiont types belonged to the same lineage but represented neither *Scytonema* nor *Chroococcus*, but a novel lineage more closely related to *Nostoc*, named *Rhizonema* (Lücking et al. 2009).

With regard to the *Dictyonema* mycobiont phylogeny, the authors noticed a striking genetic diversity of what supposedly represented only a few species (Lawrey et al. 2009), given the taxonomic concept applied to the genus at the time (largely unchanged from Parmasto's 1978 monograph). Jim and his team established the hypothesis that more than one genus was involved, the foliose species representing the genus *Cora*, and that both *Dictyonema* and *Cora* included more species than previously recognized. Using these results as a pilot study, Jim, with co-PIs Pat Gillevet and Robert Lücking, secured a large NSF grant (DEB-0841405) to study the evolution and diversification of the *Dictyonema* clade in more detail, recruiting Manuela Dal Forno as a Ph.D. student for the project. Manuela focused primarily on evolutionary aspects and photobiont relationships in the entire clade, but the project also attempted to elucidate species richness in the various genera, particularly *Cora* (using the fungal ITS barcoding locus), in close collaboration with Bibiana Moncada from the Universidad Distrital in Colombia. The first paper from Manuela's dissertation work documented the evolution of the lichen thallus in the *Dictyonema* clade, progressing from a rather undifferentiated morphology in *Cyphellostereum* and most *Dictyonema* s.str. species, to advanced and eventually highly differentiated thalli in *Acantholichen*, *Corella*, and *Cora* (Dal Forno et al. 2013). These basidiolichens thus provided a model for thallus evolution in lichen-forming fungi, even in the differential composition of bacterial microbiomes in filamentous vs. foliose lineages (Dal Forno et al. 2017).

Much to the surprise, if not to say dismay of Jim and his collaborators, the molecular phylogenetic analysis of a large number of samples of the genus *Cora* resulted not in a few but hundreds of unrecognized species, a stunning result featured on the cover of *PNAS* (Lücking et al. 2014a). The authors devised a novel method to predict global richness of the genus to over 450 species. That this number was not exaggerated was shown in a follow-up study, which only three years later recognized 184 species

Figure 8. The funny and the contemplative Jim, two personality traits that make him an outstanding colleague and teacher, and friend. A–G – At the OTS lichen courses 2007 and 2012 in Costa Rica. H – At IAL7 in Thailand 2012. Photographs by Robert Lücking except H (Manuela Dal Forno). In F he is indeed kissing a tree, honoring the tree's support of so much, almost unbearable, lichen diversity.

(Lücking et al. 2017). Further new species from Mexico are being added in this special issue dedicated to Jim (Moncada et al. 2019). To test whether these results may have been artifacts from infragenomic ITS variation, Jim and collaborators teamed up with Pat Gillevet and Masumeh Sikaroudi from Jim's home university, employing high-throughput sequencing to explore intragenomic ITS in *Cora*; they found that almost all detected variation was due to sequencing errors and that a single haplotype dominated in the genome (Lücking et al. 2014b). The level of resolution of the ITS barcoding marker was also supported by close correlation with phenotype features, including substrate ecology, habitat preference, and geographical distribution.

Expanding these studies to the other genera, Manuela and Jim found that the presumably unique lichen, *Acantholichen pannarioides*, represented at least six different species (Dal Forno et al. 2016). In collaboration with

Frank Bungartz and Alba Yánez-Ayabaca, the team also studied the diversification of the *Dictyonema* clade in the Galapagos Islands (Yánez-Ayabaca et al. 2012) and resolved all ten species occurring on the archipelago, representing four genera, as endemic (Dal Forno et al. 2017). Work to formally describe the unrecognized taxa in this clade has progressed, though somewhat slowly given the large number of species (Lumbsch et al. 2011; Lücking et al. 2013a, b, 2017; Ariyawansa et al. 2015; Dal Forno et al. 2016). This included the description of a unique, putatively hallucinogenic species of *Dictyonema* from the Ecuadorian Amazon (Schmull et al. 2014), a lichen that was initially identified by Mason Hale as undescribed *Dictyonema*, in a paper on novel hallucinogens by Davis & Yost (1983). Just another coincidence that somehow continues the circle opened with Jim's first encounter with Mason in 1976.

James Lawrey: a successful and diverse career as plant, fungal and lichen ecologist and evolutionist, with outstanding service to the scientific community

With a career in science and academics spanning nearly 45 years, Jim is as versatile a lichenologist as they come. His work continues to cover almost all topics in lichenology, from alpha-taxonomy and systematics to phylogenetics and evolution, to autecology, community ecology, biological interactions, to environmental monitoring and conservation. His methodological approaches are diverse, being an excellent field biologist, versatile with the microscope and in the lab, and always embracing the newest technological advances, such as next-generation sequencing. The authors of this tribute represent three of the generations that had the pleasure – and privilege – to get to know Jim during the various stages of his career. We certainly speak for many when we describe Jim as a very friendly and pleasant-natured person, at the same time very knowledgeable, literate and up-to-date not only in the areas of biology and lichenology, yet always funny and at the same time contemplative, thinking about new scientific questions to address (Fig. 8).

Besides having published nearly one hundred papers and book chapters, plus his much cited book *Biology of Lichenized Fungi* (Lawrey 1984), and about sixty conference abstracts, countless students had the pleasure to assist Jim's undergraduate and graduate courses on Introductory Biology, Introduction to Ecology, Plant Biology, Population Biology, Evolution, Biodiversity, Environmental Biology, Terrestrial Plant Ecology, and Lichenology, over more than forty years. Jim also participated as lecturer in both OTS lichen courses (*Tropical Lichens as Models to Study Ecological Communities Using Multivariate Techniques*) in 2007 and 2012 (Fig. 8, 9). He has been on the committees of 17 master's and 10 Ph.D. students, being the principal advisor for six of them. The three Ph.D. students advised by him reflect the broad diversity of his interests, namely plant ecology [Antoinette Pepin, 1999: *The relative importance of hydrology and substrate in the vegetation dynamics of restored freshwater wetlands*], fungal pathogens [Susan Dey Cohen, 2000: *A comparative population ecology study of the fungal pathogen Discula umbrinella* (*Syn = Discula quercina*), *on Quercus alba and Quercus rubra*], and basidiolichens, by his most recent Ph.D. student, Manuela Dal Forno, the second author of this tribute (Fig. 9). As Manuela can attest from first-hand experience, Jim possesses all characteristics of a great mentor: he is supportive, respectful, enthusiastic, understanding of difficult situations, and goes above and beyond to provide his students with the best learning opportunities. He always brings a positive attitude and provides constructive feedback (and in impressive time!). He shares his knowledge extensively and offers a lot of his time to students and those who need his help. Jim encourages everybody to utilize modern tools, to aim for interesting questions in science, and he pushes students to do their best by valuing their efforts.

Sue Cohen (Fig. 9E), his second Ph.D. student who graduated in 2000 and today is President of the Center for Regulatory Research in Roseville, Minnesota, sent us a testimony of her experience with Jim as an advisor that shows that he was an attentive an advisor back then as he continues to be today: '*Dr. James Lawrey is a fantastic doctoral advisor, mentor, and researcher. Prior to coming to George Mason University, I was working as a plant pathologist with USDA-APHIS, Riverdale, Maryland and was selected through a special USDA-APHIS program to complete my Ph.D. degree with Dr. Lawrey. I continued to work for USDA APHIS throughout my doctoral degree. I completed coursework at George Mason University while conducting research at USDA-ARS Beltsville, Maryland. Needless to say, this was a daunting task while raising a family. Dr. Lawrey was particularly great at advising and focusing on the important research issues that needed to be addressed to complete publications for my doctoral research studies.*

Table 1. Professional scientific service provided by James Lawrey over his career. ABLS = American Bryological and Lichenological Society; BLS = British Lichenological Society; BSA = Botanical Society of America; BSW = Botanical Society of Washington; IAL = International Association for Lichenology.

Years of Service	Society	Position
1986–1988	BSA	Chairman of Bryological and Lichenological Section
1987–1992	ABLS	Associate Editor, The Bryologist
1996	BSW	President
1997–2001	ABLS	Secretary/Treasurer
2001–2003	ABLS	President-Elect
2003–2005	ABLS	President
2005–2007	ABLS	Past President
2005–2009	ABLS	Advisory Committee
2005–2008	IAL	Member of IAL Council, Assistant Treasurer for North America
2005–present	BLS	Associate Editor, The Lichenologist
2012–2015	ABLS	Editor (fill out term), The Bryologist
2016–2020	ABLS	Editor (term 1), The Bryologist
2021–2025	ABLS	Editor (term 2; appointed and accepted, summer 2019), The Bryologist

Figure 9. Jim Lawrey in the field, as lecturer, advisor, and teacher. A–B. Examining tropical lichens in Costa Rica. C–D. Giving a lecture at IMC11 in Puerto Rico 2018 and with Paul Diederich at IAL8 in Asilomar in 2008. E–G. Jim's second Ph.D. student, graduated in 2000, Sue Cohen, and his most recent, graduated in 2015, Manuela Dal Forno, with colleagues Pat Gillevet and Masumeh Sikaroudi. H–J. The OTS lichen course in Costa Rica in 2012: group picture with humongous *Usnea*; discussing a field project with the students; and examining lichen UV fluorescence in situ. Group picture from above left to below right: the bus driver, José Luis Chaves, Jim Lawrey, Joel Mercado-Díaz, Emily Warschefsky, Klara Scharnagl, Alejandro Muñoz, Jessica Coyle, Matt Nelsen, Ekaphan ('Bier') Kraichak, Robert Lücking, Bibiana Moncada, Andrea Skobie, Laura Walker, Geoffrey Zahn., and Manuela Dal Forno. Photographs by Robert Lücking, except D (done by Damian Ertz), E (provided by Sue Cohen), F and G (Masumeh Sikaroodi and Morgan Gostel).

Table 2. List of taxa co-authored by Jim Lawrey.

Orders:	
	Lichenoconiales Diederich, Lawrey & K.D. Hyde
	Lichenostigmatales Ertz, Diederich & Lawrey
Families:	
	Lepidostromataceae Ertz, Eb. Fisch., Killmann, Sérusiaux, & Lawrey
	Lichenoconiaceae Diederich & Lawrey
Genera:	
	Adamflakia Diederich & Lawrey
	Briancoppinsia Diederich, Ertz, Lawrey & van den Boom
	Burgella Diederich & Lawrey
	Burgellopsis Diederich & Lawrey
	Eonema Redhead, Lücking & Lawrey
	Lichenobarya Diederich, Etayo & Lawrey
	Marchandiomphalina Diederich, Lawrey & Binder
	Muscinupta Redhead, Lücking & Lawrey
Species:	
	Adamflakia applanata (Diederich, Flakus & Etayo) Diederich & Lawrey
	Briancoppinsia cytospora (Vouaux) Diederich, Ertz, Lawrey & van den Boom
	Burgella flavoparmeliae Diederich & Lawrey
	Burgellopsis nivea Diederich & Lawrey
	Burgoa angulosa Diederich, Lawrey & Etayo
	Ceratobasidium bulbillifaciens Diederich & Lawrey
	Cora barbulata Lücking, Dal-Forno & Lawrey
	Cora hymenocarpa Lücking, Chaves & Lawrey
	Cora imi Lücking, Chaves & Lawrey
	Corella melvinii (Chaves, Lücking & Umaña) Lücking, Dal-Forno & Lawrey
	Corticium silviae Diederich, E. Zimm. & Lawrey
	Cyphellostereum phyllogenum (Müll. Arg.) Lücking, Dal-Forno & Lawrey
	Dictyonema gomezianum Lücking, Dal-Forno & Lawrey
	Dictyonema hernandezii Lücking, Lawrey & Dal-Forno
	Dictyonema huaorani Dal-Forno, Schmull, Lücking & Lawrey
	Dictyonema phyllophilum (Parmasto) Lücking, Dal-Forno & Lawrey
	Dictyonema metallicum Lücking, Dal-Forno & Lawrey
	Laetisaria buckii (Diederich & Lawrey) Diederich & Lawrey
	Laetisaria culmigena (R.K.Webster & D.A.Reid) Diederich & Lawrey
	Laetisaria lichenicola Diederich, Lawrey & Van den Broeck
	Laetisaria marsonii (Diederich & Lawrey) Diederich & Lawrey
	Laetisaria nothofagicola (Diederich & Lawrey) Diederich & Lawrey
	Laetisaria roseipellis (Stalpers & Loer.) Diederich & Lawrey
	Lepidostroma akagerae (Eb. Fisch., Ertz, Killmann & Sérus.) Ertz, Eb. Fisch., Killmann, Sérus. & Lawrey
	Lepidostroma rugaramae (Eb. Fisch., Ertz, Killmann & Sérus.) Ertz, Eb. Fisch., Killmann, Sérus. & Lawrey
	Lichenobarya usneae (Etayo) Diederich, Etayo & Lawrey
	Lichenoconium aeruginosum Diederich, M. Brand, van den Boom & Lawrey
	Marchandiomphalina foliacea (P.M. Jørg.) Diederich, Lawrey & Binder
	Marchandiomyces buckii Diederich & Lawrey
	Marchandiomyces lignicola Lawrey & Diederich
	Marchandiomyces marsonii Diederich & Lawrey
	Marchandiomyces nothofagicola Diederich & Lawrey
	Minimedusa obcoronata (B. Sutton, Kuthub. & Muid) Diederich & Lawrey
	Minimedusa pubescens Diederich, Lawrey & Heylen
	Muscinupta laevis (Fr.:Fr.) Redhead, Lücking & Lawrey
	Neoburgoa freyi Diederich, Zimmermann & Lawrey
	Phoma puncteliae Diederich & Lawrey

I am pleased to see Dr. Lawrey recognized for his wonderful academic contributions and professional society service this year in the upcoming special issue.' (Sue Cohen, pers. comm. Nov. 2019).

While Jim pursued his successful career in scientific research and mentoring students, he also expanded his scope to include broader service to his scientific discipline, along the way fostering bryology as well as lichenology (Table 1). He began in the late 1980s by serving as Chairman of Bryological and Lichenological Section of the Botanical Society of America and as Associate Editor for *The Bryologist*, the primary official journal of the American Bryological and Lichenological Society (ABLS). In this capacity, he published a number of highly useful book reviews for the journal (Lawrey 1986b, 1988, 1990, 1993c, 1994a–c, 1995c, d, 1996). Such reviews are usually listed in less important sections of a curriculum, but in Jim's case they demonstrate his broad interest and reflect his career development, including books on lichen ecology, pollution, algal symbioses, plant-animal interactions, quantitative approaches to the characterization of vegetation and statistical methods in biology, and even the beautiful coffee-table book co-authored by the late Gillean T. Prance on tree barks around the world (Sandved et al. 1993).

After a short hiatus Jim served ABLS for 10 years (1997–2007) as a member of the Executive Committee.

Figure 10. Selected taxa co-authored by James Lawrey. A – *Burgella flavoparmeliae*. B – *Minimedusa pubescens*. C – *Marchandiomphalia* (*M. foliacea*, now considered a species of *Agonimia*). D – *Dictyonema hernandezii*. E – *Cora imi*. F – *Lepidostromataceae* (*Lepidostroma calocerum*). Photos: P. Diederich (A–B), R. Lücking (C–F).

He kept the society connected and solvent as Secretary/Treasurer, organized successful meetings as President-Elect, and guided the society as President. In those capacities he helped foster the careers of both bryologists and lichenologists, as well as maintaining the society's welcome for amateurs as well as professionals in both disciplines. Not satisfied with that, upon invitation by Senior Editor Peter Crittenden, in early 2006 Jim became an Associate Editor for *The Lichenologist*, the official journal of the British Lichen Society – a position that continues. As Peter revealed to us in a personal communication, he regards Jim's contribution to *The Lichenologist* as invaluable, both in his handling of papers as an Associate Editor and in providing 'wise counsel' in relation to problematic submissions. Apparently Jim was still not busy enough: in 2012 he accepted the strictly voluntary position of Editor for *The Bryologist* to fill out someone else's term, next accepted an offer for his own five-year term, and has recently accepted an offer for a second five-year term, meaning 31 issues as Editor with >450 contributions and counting. In this capacity, Jim has played a special role in fostering the careers of both bryologists and lichenologists with publication success. In his first year he expanded the stable of Associate Editors from four to ten, to better serve contributing authors. He has continued the earlier expansion of the scope of the journal beyond its original North American focus to strongly cover both Americas as well as the entire rest of the globe. Under his supervision the journal has gone online as well as in print; its production management has improved; its range of content type has broadened to include major classification papers; and its standing in the scientific world has increased. Jim has shown unfailing patience and kindness to authors while at the same time unflinchingly maintaining high standards of scientific writing. In collaboration with associate editors, he has spent countless hours working directly with authors to bring publications up to his standards (as the authors of this paper well know from personal experience!), and he has a reputation for some of the most polite and encouraging rejections in the fields.

When Jim became Editor of *The Bryologist* in 2012, he offered to remain on the board of *The Lichenologist* to keep in touch with its progress. Since then, while acting as Editors of the two flagship journals in lichenology, Peter and Jim would get together at conferences over a beer or coffee to compare notes on how the two journals were progressing and responding to current challenges, a reflection of Jim's open and collegiate nature. At one time, during the BLS editorial dinner at the IMC11 in Puerto Rico in 2018, Peter would proudly report a substantial increase of the impact factor of *The Lichenologist* from 2016 to 2017, only to acknowledge that (and to wonder how) *The Bryologist* had done even better. Indeed, the 2018 volume of *The Bryologist* reached its highest ever impact factor, 2.368 – a great achievement for a society as small as ABLS (~500 members).

Jim has also served as panel member for the National Science Foundation in their EP-DDIG, Systematic Biology, and Evolutionary Ecology programs, and as external reviewer for grant agencies in the USA, Canada, Mexico, Iceland, Austria, the Czech Republic, Estonia, and Israel. Besides these services, Jim provided peer reviews for over 30 journals, including such diverse titles as *Allelopathy Journal*, *American Journal of Botany*, *Bioresource Technology*, *Biotropica*, *Canadian Journal of Botany*, *Ecology*, *Environmental and Experimental Botany*, *Evolution*, *Functional Ecology*, *Fungal Biology*, *Fungal Diversity*, *International Journal of Plant Science*, *Journal of Chemical Ecology*, *Journal of Plant Interactions*, *Molecular Phylogenetics and Evolution*, *Mycologia*, *Mycological Progress*, *Mycological Research*, *New Phytologist*, *Plant Biology*, *Proceedings of the National Academy of Sciences of the USA*, *Soil Science Society of America Journal*, *Symbiosis*, and *Systematic Botany*. Clearly Jim is not just a productive and efficient scientist but must also be one of the most energetic. We are in awe of how he has done it so well and wish him many more years with this level of energy!

Being primarily a lichen ecologist and specialist in the biology of lichenicolous fungi, Jim has also been involved in the systematics and taxonomy of these organisms, having co-authored two new orders, two new families, eight new genera, and 37 species including combinations (Table 2). One genus of lichenicolous fungi has so far been named after Jim, *Lawreymyces* Lücking & Moncada, although the jury is still out on the status of this name. The latter name has been proposed for a basidiomycete fungus growing cryptically in the thalli of a macrosquamulose

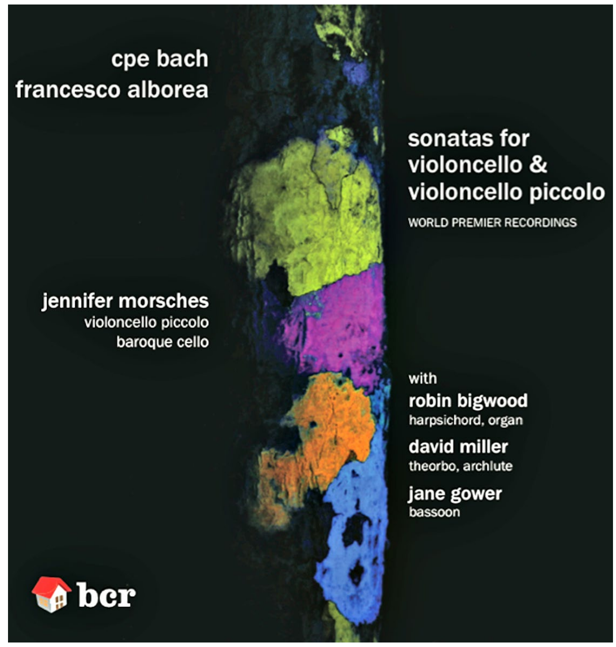

Figure 11. Lichen UV fluorescence featured on the cover of cellist Jennifer Morsches album *CPE Bach and Francesco Alborea: Sonatas for violoncello & violoncello piccolo* (© 2014 Barn Cottage Records). Reproduced with permission by Jennifer Morsches, who sends her warmest regards.

Agonimia (Lücking & Moncada 2017), which based on sequences of that fungus had previously been considered a novel genus, *Marchandiomphalina*, co-authored by Jim (Lawrey et al. 2008). In this issue honoring Jim's career, which now spans 46 years after obtaining his master's degree in 1973, two genera and four species are dedicated to him: *Lawreya* Ertz, Common, Diederich & U. Braun, *Lawreyella* Flakus, Etayo, Kukwa & Rodr. Flakus, *Cora lawreyana* Moncada, R.-E. Pérez & Lücking, *Cyphellostereum jamesianum* Dal Forno & Kaminsky, *Dictyonema lawreyi* Dal Forno, Kaminsky & Lücking, and *Parmotrema lawreyi* Bungartz & Spielmann.

To highlight just one anecdote from Jim's personal life: his sister-in-law is the renowned cellist Jennifer Morsches and, not unexpectedly, she got hooked on lichens, too (Jim is indeed contagious that way). When publishing her 2014 album *CPE Bach and Francesco Alborea: Sonatas for violoncello & violoncello piccolo* (Barn Cottage Records), Jennifer used a picture of UV-fluorescent lichens taken during the OTS lichen course in 2007 in Costa Rica as cover image (Fig. 11), taking it as an example how to perceive art: '*In our desire to label and classify things, we often overlook the intrinsic qualities and farreaching possibilities of an object begging to be uncovered. Perhaps the 'anomaly' of the piccolo cello is simply our confusing attempt to categorize this rare instrument as a one-time wonder, suitable for a few select pieces. My research on its repertoire, the vibrant historical players I discovered, how they shared and responded amongst themselves, the layers of my instrument's provenance and my interactions with other musicians on this subject have proved otherwise*.' (Morsches 2013: 38). She continues stating that under UV fluorescence, the '… *lichen and its various molecular properties explode into* *colour. Similarly, by uncovering layers of a composer's work, or the luthier's vibrating musical box or a painter's canvas, the channels through which they share their craft and their inspiration present a much more complex work of art. Through the communication of their oeuvre, we too look for our preferences, our dreams and even our distant memory. No matter if the observer is an amateur, a specialist, or a passer-by, the experience is enriched*.' (Morsches 2013: 39). The awesome effect of lichen UV fluorescence, another sideline of their diverse chemistry, is indeed perhaps the most popular tool to get people interested in these organisms, as Jim vividly experienced during the OTS lichen courses in Costa Rica, documented in a popular article co-authored by him in *Fungi Magazine* (Lücking et al. 2014). From lichen chemistry to outreach: another circle completed.

James D. Lawrey: Structured list of publications

Master and Doctoral dissertation works and resulting publications, focusing on plant and fungal ecology and impact of heavy metals from coal strip-mining (1973–1979)

Lawrey, J. D. 1973. *The Missouri River Floodplain Communities from Yankton, South Dakota, to Rulo, Nebraska: Their Successional and Geographic Relationships, and Effects of River Bank Stabilization*. Master's Dissertation, University of South Dakota, Vermillion, U.S.A.

Lawrey, J. D. & Rudolph, E. D. 1975. Lichen accumulation of some heavy metals from acidic surface substrates of coal mine ecosystems in southeastern Ohio. *The Ohio Journal of Science* 75: 113–117.

Lawrey, J. D. 1977a. *Litter Decomposition and Trace Metal Cycling Studies in Habitants Variously Influenced by Coal Strip-Mining*. Doctoral Dissertation, The Ohio State University, Columbus, U.S.A. https://etd.ohiolink.edu/pg_10?::NO:10:P10_ETD_SUBID:133041

Lawrey, J. D. 1977b. X-ray emission microanalysis of *Cladonia cristatella* from a coal strip-mining area in Ohio. *Mycologia* 69: 855–860.

Lawrey, J. D. 1977c. The relative decomposition potential of habitats variously affected by surface coal mining. *Canadian Journal of Botany* 55: 1544–1552.

Lawrey, J. D. 1977d. Soil fungal populations and soil respiration in habitats variously influenced by coal strip-mining. *Environmental Pollution* 14: 195–205.

Lawrey, J. D. 1977e. Elemental partitioning in *Pinus resinosa* leaf litter and associated fungi. *Mycologia* 69: 1121–1128.

Lawrey, J. D. 1978a. Nutrient element content of terricolous cryptogams from a coal strip-mining area in Ohio. *Bulletin of the Torrey Botanical Club* 105: 201–204.

Lawrey, J. D. 1978b. Trace metal dynamics in decomposing leaf litter in habitats variously influenced by coal strip mining. *Canadian Journal of Botany* 56: 953–962.

Lawrey, J. D. 1979. Boron, strontium, and barium accumulation in selected plants and loss during leaf litter decomposition in areas influenced by coal strip mining. *Canadian Journal of Botany* 57: 933–940.

Lichen ecology and pollution monitoring using lichens, focusing on long term plots and work for the National Park Service (1976–2011)

Slocum, R. D. & **Lawrey, J. D.** 1976. Viability of the epizoic lichen flora carried and dispersed by green lacewing (*Nodita pavida*) larvae. *Canadian Journal of Botany* 54: 1827–1831.

Lawrey, J. D. & Hale, M. E. Jr. 1977. Natural history of Plummers Island, Maryland XXIII. Studies on lichen growth rate at Plummers Island, Maryland. *Proceedings of the Biological Society of Washington* 90: 698–725.

Lawrey, J. D. & Hale, M. E., Jr. 1979. Lichen growth response to stress induced by automobile exhaust pollution. *Science* 204: 423–424.

Lawrey, J. D. 1980a. Sexual and asexual reproductive patterns in *Parmotrema* (Parmeliaceae) that correlate with latitude. *The Bryologist* 83: 344–350.

Lawrey, J. D. & Hale, M. E. Jr. 1981. Retrospective study of lichen lead accumulation in the northeastern United States. *The Bryologist* 84: 449–456.

Lawrey, J. D. 1981. Evidence for competitive release in simplified saxicolous lichen communities. *American Journal of Botany* 68: 1066–1073.

Hale, M. E. Jr. & **Lawrey, J. D.** 1985. Annual rate of lead accumulation in the lichen *Pseudoparmelia baltimorensis*. *The Bryologist* 88: 5–7.

Lawrey, J. D. 1987. Nutritional ecology of lichen/moss arthropods. In: Slansky, F. & Rodriguez, J. G. (eds), *Nutritional Ecology of Insects, Mites, and Spiders*, pp. 209–233. John Wiley & Sons, New York.

Lawrey, J. D. & Hale, M. E. Jr. 1988. Lichen evidence for changes in atmospheric pollution in Shenandoah National Park, Virginia. *The Bryologist* 91: 21–23.

Lawrey, J. D. 1991a. The species-area curve as an index of disturbance in saxicolous lichen communities. *The Bryologist* 94: 377–382.

Lawrey, J. D. 1991b. Biotic interactions in lichen community development: a review. *The Lichenologist* 23: 205–214.

Lawrey, J. D. 1992. Natural and randomly-assembled lichen communities compared using the species area curve. *The Bryologist* 95: 137–141.

Lawrey, J. D. 1993a. Lichens as monitors of pollutant elements at permanent sites in Maryland and Virginia. *The Bryologist* 96: 339–341.

Lawrey, J. D. 1993b. *Lichen Biomonitoring Program in the Dolly Sods and Otter Creek Wildernesses of the Monongahela National Forest: A Resurvey of Lichen Floristics and Elemental Status*. Final report to the Forest Supervisor, Monongahela National Forest, USDA Forest Service.

Lawrey, J. D. 2011. *A Lichen Biomonitoring Program to Protect Resources in the National Capital Region by Detecting Air Quality Effects*. Natural Resource Technical Report NPS/NCRN/NRTR—2011/450. National Park Service, Fort Collins, CO, USA. https://irma.nps.gov/DataStore/DownloadFile/428476 [accessed 5 April 2019]

Lichen chemical ecology (1977–1995)

Lawrey, J. D. 1977f. Adaptive significance of *O*-methylated lichen depsides and depsidones. *The Lichenologist* 9: 137–142.

Lawrey, J. D. 1977g. Inhibition of moss spore germination y acetone extracts of terricolous *Cladonia* species. *Bulletin of the Torrey Botanical Club* 104: 49–52.

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Outreach

Lücking, R., Dal Forno, M., Moncada, B., Chaves, J. L. & **Lawrey, J. D.** 2014. The enchanted jungle. Fungi Magazine 7: 28–31.

Acknowledgements

We thank Lowell Adams, Larry St. Clair, Sue Cohen, Paul Diederich, Pat Gillevet, Matt Perry, Larry Rockwood, Amy Rossman, Masumeh Sikaroodi, Judith Skog, and Albert Torzilli for placing information on Jim's career, data and pictures at our disposal. Even Jim did, although without knowing.

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