



Review

Chronicle of Research into Lichen-Associated Bacteria

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Abstract: Lichens are mutually symbiotic systems consisting of fungal and algal symbionts. While diverse lichen-forming fungal species are known, limited species of algae form lichens. Plasticity in the combination of fungal and algal species with different eco-physiological properties may contribute to the worldwide distribution of lichens, even in extreme habitats. Lichens have been studied systematically for more than 200 years; however, plasticity in fungal–algal/cyanobacterial symbiotic combinations is still unclear. In addition, the association between non-cyanobacterial bacteria and lichens has attracted attention in recent years. The types, diversity, and functions of lichen-associated bacteria have been studied using both culture-based and culture-independent methods. This review summarizes the history of systematic research on lichens and lichen-associated bacteria and provides insights into the current status of research in this field.

Keywords: lichen–bacterial association; symbiosis; culture; DNA sequencing; -omics

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1. Introduction

According to one version of the story, the term “lichen” originated from the Greek “λεϊχήν” (leichen), meaning “licker”, and was later transcribed to “lichen” [1]. The approximately 20,000 lichen species are highly mutually symbiotic systems consisting of fungal and algal symbionts. Lichen nomenclature is based on lichen-forming fungal species. Although ~20,000 lichen-forming fungal species are known, only a few species of algae from two green algal genera, *Trebouxia* and *Cocomyxa*, form lichens. Plasticity in the combination of fungal–algal species having different eco-physiological properties may contribute to the worldwide distribution of lichens, even in maritime and extreme habitats, covering approximately 8% of Earth’s land surface [2–5]. Lichens have been studied systematically for over 200 years [6], but plasticity in fungal–algal symbiotic combinations remains unclear [7].

Lichen-like symbioses presumably developed characteristic growth styles approximately 600 million years ago [8]. Linnaeus initially classified lichens as algae [6], but this view was challenged after the discovery of “gonidia” by Wallroth in 1825 [9]. In 1867, Schwendener proposed the basic recognition of the dual association between fungi and algae [10]. Further, in 1876, Frank first proposed the concept of “symbiosis” and used it to describe lichens [11]. Moreover, in 1879, de Bary also used the concept of “symbiosis” in his book “Die Erscheinung der Symbiose” and carried this concept forward [12]. Lichens are believed to be the symbiosis of fungi and algae. Cyanobacteria were discovered as another type of photobiont closely associated with nitrogen fixation in lichens [13]. At present, approximately 20,000 lichen species have been described, most of which have algal partners as photobionts; however, only 10% of lichens are symbiotic with cyanobacteria. Approximately 2–4% of lichen-forming fungi are associated with both algal and cyanobacterial phototrophs [4,14]. Further, >2000 species of obligate lichenicolous fungi, which are not lichen-forming but lichen-parasitic, have been identified [15].

Lichens play a unique role in many spheres. For example, lichens serve as pioneer organisms in the primary succession of ecological communities [16]. They help prevent desertification and restore desert by forming a biological crust or biocrust [17–19]. Owing to their sensitivity to environmental changes, lichens can be used as a biological indicator to evaluate and monitor the extent of air pollution [20,21]. Further, lichens facilitate the measurement of the surface age of exposed rocks based on their growth on some exposed rocks [22]. Lichens decompose polyester resins, heavy metals, radionuclides, other pollutants, and certain pathogens; consequently, they help purify the environment [23–25]. Lichens serve as food for some animals in the wild [26]. Some lichen species, with beneficial health effects on humans, are used as a food source [27]. Lichens are also used to prepare dyes and perfumes [28,29]. Lichens are reportedly used in traditional medicinal preparations [30]. A study provided chemical and biological evidence for the ethnopharmacological uses of *Flavoparmelia caperata* against alcohol-induced hepatic injury [31]. Lichens produce metabolites possessing antibacterial and anti-inflammatory activities [32,33].

Biochemical and biomedical aspects are often presumed to be related to the fungal activity; however, the roles or functions of bacteria, whether symbiotic or merely associated, cannot be ruled out. This mini-review chronicles studies on lichen-associated bacteria, focusing on methodologies from classical culture-based approaches to modern culture-independent challenges, including “-omics”, with a brief mention of artificial infection.

2. Discovery of Other Symbiotic Components

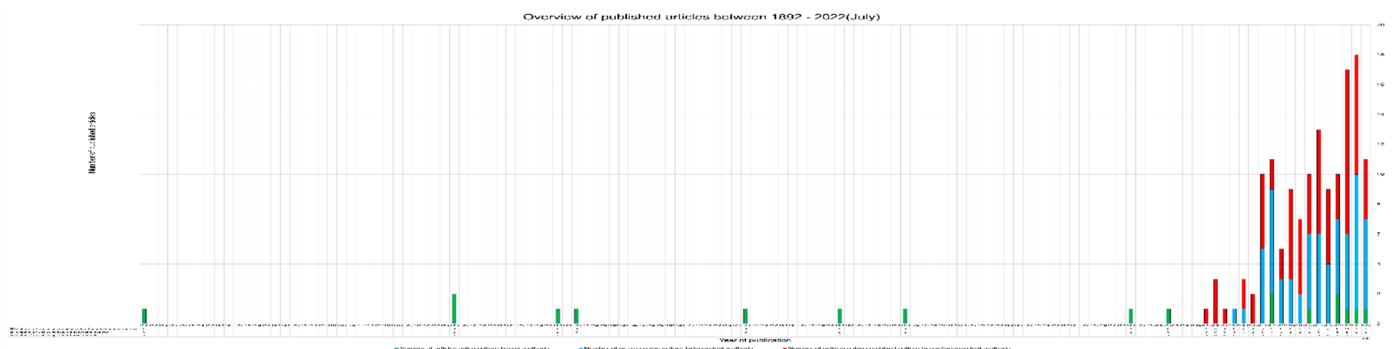
Although lichens were initially thought to be the symbiosis of fungi and algae (or cyanobacteria), an increasing number of subsequent studies have shown that lichens are not simply binary or ternary symbionts such as bacteria, yeasts, protists, or viruses [34–37]. Therefore, some researchers refer to lichens as “holobionts” dominated by certain fungi containing a variety of microbiomes [38] and redefine lichens as a self-sufficient ecosystem formed by the interaction of a thallus-forming fungus, an extracellular arrangement of one or more photosynthetic partners, and a variable number of other microorganisms [39]. In this case, each organism has its niche in the complex lichen ecosystem and may grow on its own under certain natural or artificial conditions. Therefore, the “lichen” phenotype can be considered a symbiotic phenotype of lichen-forming fungi, which is in accordance with current research results [40]. Lichens of artificial recombinant fungal/algal partners with different properties can be generated and assessed for phenotypic features [41,42].

This review focuses on lichen-associated bacterial research in recent years. The isolation of bacteria from lichens has a century-long history. As early as 1892, Thaxter isolated the deltaproteobacterial *Chondromyces lichenicolus* (currently *Melittangium lichenicola* [43]) from lichens [44]; this may be the first bacterium to have been isolated from lichens according to existing records. In the 20th century, there was no consensus that bacteria were symbionts of lichens, but researchers successively isolated bacteria of various genera, including *Azotobacter* [45,46], *Pseudomonas* [47], *Bacillus* [47], *Beijerinckia* [48], and *Clostridium* [46] from lichens. In 1925, Uphof isolated a purple bacterium from *Chiodecton sanguineum* (now *Cryptothecia rubrocincta* [49]) and named it *Rhodobacterium lichenophora*. He also renamed *Chiodecton sanguineum* to *Rhodobacteriophora sanguinea* [50,51]. Although the relevant literature is still cited today, it should be noted that in 1926, Succsenguth came to different conclusions in his research results and doubted the results of Uphof [52]. Grube et al. suspected a misunderstanding of secondary crystalline compounds in these two contradictory reports [53]. To date, there have been no follow-up studies or data on purple bacteria. Lichen-associated bacteria have been isolated and detected for a long time, but until the first few years of the 21st century, some researchers still referred to them as epiphytic bacteria or even bacterial contamination [54,55].

3. Research Methods Involving Lichen-Associated Bacteria

If contradictory reports stem from a single research method at the time, subsequent research methods combined with molecular methods considerably reduce the possibility of such contradictions. Currently, research methods for lichen-associated bacteria can be roughly divided into culture-based and culture-independent methods. Culture-based methods are used to isolate and cultivate bacteria from lichens and include various physical and chemical experimental methods to study the structure, function, products, and metabolites of bacteria. Culture-independent methods include molecular methods, such as DNA extraction, polymerase chain reaction (PCR), gel electrophoresis, and denaturing gradient gel electrophoresis (DGGE). First-generation DNA sequencing (Sanger method) and shotgun sequencing have been used to identify the isolated bacteria and perform whole-genome sequencing. Second-generation sequencing, also known as high-throughput or next-generation sequencing (NGS) (for example, 454-pyrosequencing, Illumina sequencing, and Ion Torrent sequencing), third-generation sequencing, also known as long-read sequencing (Single-Molecule Real-Time (SMRT) sequencing), and -omics technologies have only recently been used to study lichens for the identification and analysis of isolated bacteria, as well as for the compositional and functional analysis of bacterial communities.

An extensive list of studies on lichen-associated bacteria since 1892 is shown in Table S1 and categorized based on culture-based, culture-independent, and combined methods [39,44–48,50,51,55,56–197]. The yearly numbers of corresponding publications are shown in Figure 1.



(A)

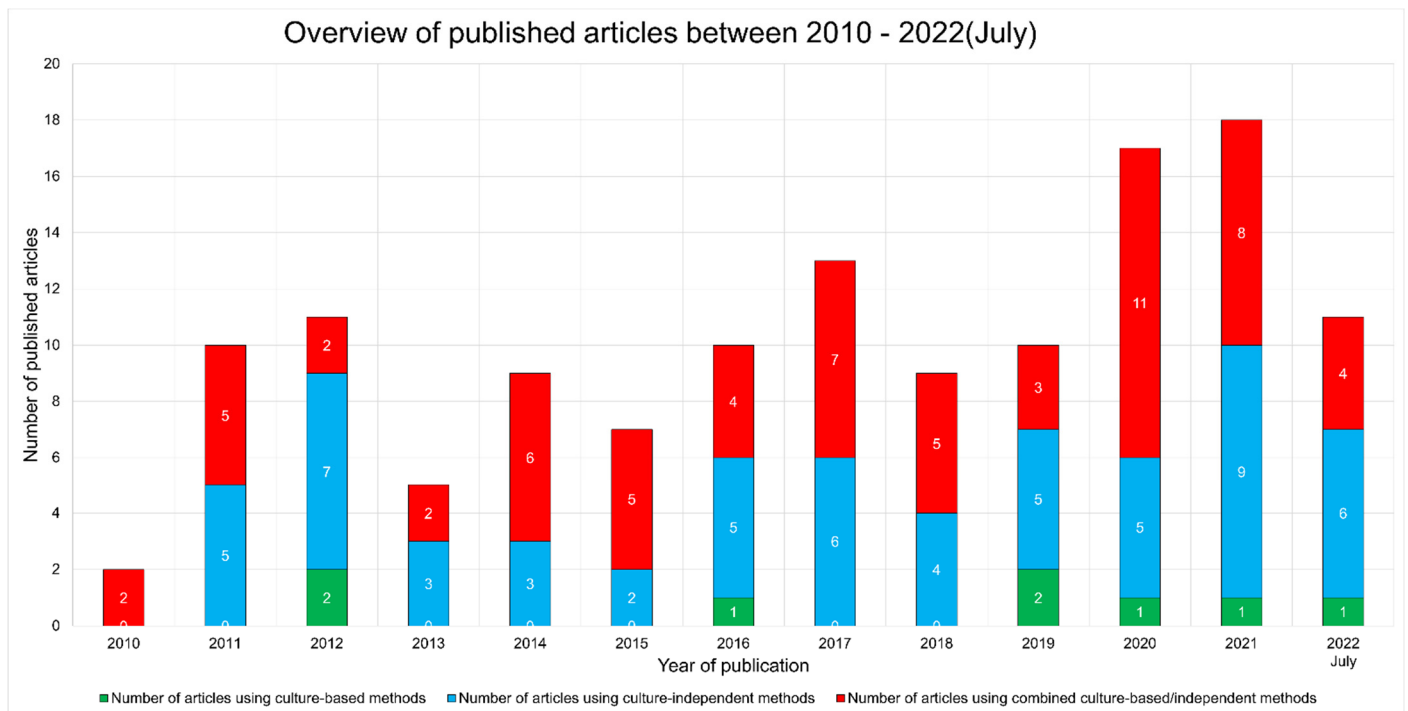


Figure 1. Yearly numbers of publications are listed in Table 1, as categorized by culture-based, culture-independent, and combined methods. (A) numbers of publications from 1892 to July 2022. (B) numbers of publications from 2010 to July 2022.

According to our review, the first research paper concerning the analysis of lichen-associated bacteria by culture-independent methods appeared in 2005; before that, a few existing studies on lichen-associated bacteria employed culture-based methods. In addition, in the same year, Cardinale et al. published research on the bacterial communities of several different lichens [198], which may represent the first report on bacterial communities, and published a related paper in 2006 [34]. In 2006, a study by Liba et al. first used Sanger DNA sequencing to analyze isolated nitrogen-fixing bacteria on a large scale [193], assuming that bacteria exist as symbionts. In 2008, Cardinale et al. pioneered the use of FISH to analyze bacterial communities in lichens, which was the first study to use only culture-independent methods [191]. In 2011, Mushegian et al. used second-generation sequencing methods (454-pyrosequencing) combined with Terminal Restriction Fragment Length Polymorphism analysis (T-RFLP) to analyze lichen bacterial communities [179]. In the same year, Schneider et al. pioneered the use of meta-proteomics to analyze the function of lichen-associated bacteria, which was the first to rely on culture-independent methods to analyze the function of lichen-associated bacteria [178]. In subsequently published papers, many researchers have used a variety of culture-independent methods to analyze the functions of lichen-associated bacteria; however, the culture-independent methods chosen by most researchers were similar to those described above.

After discovering the suitability of culture-independent methods for studying lichen-associated bacteria, most studies gradually selected new techniques for culture-independent methods. Among the associated papers referenced in this review, 88.1% used culture-independent methods to study lichen-associated bacteria, which is close to 95% considering the emergence and generalization time of the technology. Perhaps, considering convenience and accuracy, many researchers have abandoned culture-based methods and devoted themselves to culture-independent research. Papers that reported only culture-based or culture-independent methods accounted for 11.9% and 41.1% of

the total, respectively. Papers that used both methods accounted for 47.0% of the total. A taxonomic summary of publications using culture-based, culture-independent, and combined methods is presented in Table 1.

Table 1. A list of 151 publications on the isolation or analysis of lichen-associated bacteria, categorized based on culture-based, culture-independent, and combined methods. Detected major phyla are listed. The numbers of all relevant publications and publications using culture-based, culture-independent, and combined methods are shown.

Phylum	Total Number of Publications	Number of Publications Using Culture-Based Methods	Number of Publications Using Culture-Independent Methods	Number of Publications Using Combined Culture-Based/Independent Methods
<i>Pseudomonadota</i>	103	50	51	2
<i>Actinomycetota</i>	59	40	19	0
<i>Bacteroidota</i>	27	13	14	0
<i>Acidobacteriota</i>	25	0	25	0
<i>Bacillota</i>	21	15	6	0
<i>Cyanobacteria</i>	8	0	8	0
<i>Gemmatimonadetes</i>	1	0	1	0
<i>Planctomycetota</i>	1	0	1	0

Lichen species and lichen-associated bacteria studied since 1892 are shown in Table S1. Lichen species were as accurate as possible at the species level. To facilitate the statistics of the types of related bacteria, this review classifies all bacteria studied using culture-based and culture-independent methods at the phylum level, and the phylum names are based on the latest validation [199]. A total of 145 of 151 publications reported isolation or analysis of specific species of lichen-associated bacteria using culture-based or culture-independent methods or both. Several interesting results were obtained. Among them, eleven publications reported culture-based methods for isolating *Actinomycetota*, probably because their functions have attracted the interest of researchers. Strains of *Pseudomonadota* were isolated and analyzed, as indicated in two publications, using both culture-based and culture-independent methods. *Pseudomonadota* was identified in 69.5% of all the publications and regarded as the dominant phylum. Of the 103 publications that isolated or detected *Pseudomonadota*, almost half used culture-based and culture-independent methods. The second most dominant phylum was *Actinomycetota*, accounting for 40.7% of all the publications. The phyla *Bacteroidota* and *Bacillota* were identified using both culture-based/independent methods, whereas *Acidobacteriota* was identified only using culture-independent methods. *Cyanobacteria* was mostly identified using metagenomics or in some publications without deletion of related sequences. *Gemmatimonadetes* and *Planctomycetota* were reported as dominant phyla once in two different publications in 2020 and 2012, respectively.

4. Problems and Challenges

Culture-independent molecular methods, such as high-throughput sequencing tools, reveal the species diversity of unexplored microbial communities and reveal the presence of many novel microorganisms previously undetectable by culture-based methods. These methods rely on culture-independent methods to directly analyze the function of lichen-associated bacteria. Culture-based methods are critical for the discovery of useful bioactive compounds. Combined with molecular techniques, the identification of isolated strains and analysis of metabolites have been greatly facilitated, with a reduced possibility of errors. In addition, some researchers insist on using only culture-based methods to analyze bacteria.

However, it is worth noting that methodological variety has, rather unfortunately, resulted in some drawbacks due to methodological non-uniformity. For example, different media used in culture-based methods have isolated different strains, leading to different results when evaluating the numbers and diversity of lichen-associated bacteria. Therefore, some researchers have used various media simultaneously to lessen the impact of this issue. In addition, some researchers have used both culture-based and culture-independent molecular methods to evaluate the number and diversity of lichen-associated bacteria. Pankratov et al. pointed out that no correlations are seen between the cultured bacteria and molecular genetic information of lichen-associated bacteria [200].

A major challenge in lichen-associated microbiology is the prediction of the roles or functions of bacteria in lichens. Pankratov et al. concluded that the most obvious functions of the bacterial communities in lichens are: (1) nitrogen fixation; (2) production of secondary metabolites, such as growth regulators, vitamins, antibiotics, ethylene, and indole acetic acid, as well as the production of “lichenic acid”; (3) degradation of thallus and migration of macro and trace elements to lichen growth sites; (4) formation of carbohydrate pools as polysaccharides of bacterial origin [200]. Studies concerning the functions of lichen-associated bacteria are listed in Table S1 by publications dating back to 1892, including all data that can be found, which is essentially consistent with the above-mentioned summary [39,44–48,50,51,55–197]. Many researchers have been interested in the functions of *Actinomycetota*. None of these functions is unique to lichens; bacteria also exhibit some of these functions, whether they are symbiotic/associated with other organisms or live alone. Most importantly, there have been no complete experiments or evidence to determine the roles of bacteria in lichens, and researchers usually make assumptions based on the featured functions of isolated bacteria or known functions of relevant taxa. Increasing the accuracy of such assumptions is an urgent issue, particularly when employing culture-independent methods and omics or meta-omics.

An unprecedented challenge in lichenology is the artificial infection of a selected bacterium or a set of selected bacteria to pre-sterilized lichens. Agarwood (*Aquilaria malaccensis*) exemplifies artificial inoculation. Its endophytic fungal/bacterial isolates are inoculated to enhance the production of natural incense [201]. Agarwood surface is pre-sterilized with ethanol and sodium hypochlorite [202]. Lichens are also surface-sterilized with ethanol, sodium hypochlorite, or hydrogen peroxide [203,204], but artificial infection against lichens has still been an intriguing challenge.

5. Conclusions

Lichens have been systematically studied for over 200 years, but their nature remains poorly understood, particularly plasticity in fungal–algal symbiotic combinations. As to bacterial associates of lichens, traditional culture-based methods reveal their physiological and biochemical features *in vitro* but allow only inferences on their roles *in vivo* in lichens. Culture-independent molecular approaches provide taxonomic and phylogenetic identifications of bacterial associates but only *in silico* speculations on their functions in lichens. Considering the variety and practicality of secondary metabolites produced by lichen-forming fungi and bacteria, lichen-associated bacteria would represent huge treasure houses for human benefit. However, research on lichen-associated bacteria is still limited. For research methods targeting lichen-associated bacteria, the publications found and summarized in this review do not necessarily cover all, and related studies are urgently needed to develop a more complete and accurate understanding. Overall, much remains to be accomplished in advancing research on lichen-associated bacteria.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/microorganisms10112111/s1>, Table S1: Total of 151 original articles on lichen-associated bacteria research since 1892 to 2022 (July) by descending order, including 145 original papers, 4 theses and 2 reports. The subjects, methods, information of lichen samples, phyla and analyzed functions of isolated bacteria based on different methods are listed in the table are only those-associated to bacteria respectively

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