

Functions of Microbial Pigments

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Microbial pigments play multiple roles in the ecosystem construction, survival, and fitness of all kinds of organisms. Considerably, microbial (bacteria, fungi, yeast, and microalgae) pigments offer a wide array of food, drug, colorants, dyes, and imaging applications.

Microbial Pigments

biological properties

fluorescent pigments

1. Introduction

The survival of life forms on earth is dependent on various pigments, including light-harvesting pigments like chlorophylls, phycoerythrin, and phycobiliproteins [1][2]; harmful light-filtering pigments like proteorhodopsins [3][4], melanin's, pyomelanin, pyocyanin, fluorescent proteins; predator defending pigments like aplsinoviolin [5], cephalopods ink [6][7], Dendrobatidae frog toxins [8], microbial pigments and so on [9]. The quantity, quality, and attractiveness of pigments from various sources such as microbes, algae, invertebrates, and macro-organisms may comprise either beneficial or toxic chemical constituents. Not all colors appealing to our eyes are beneficial to humans. Therefore, investigations on the chemistry of pigment molecules are gaining more interest in the current research. In 1666, Sir Isaac Newton had initiated the beginning of research on colors by developing the first circular diagram of colors, and later various researchers like Harris (1776) and Goethe (1810). Sir Humphry Davy demonstrated the causes of various colors of organic molecules [10]. Later in 1820, Friedrich Accum revealed the many side effects of synthetic colorants in various foods [11]. Sir William Henry Perkin was the first man to develop the first synthetic textile color compound "mauve" in 1856. With this brief historical background, the visible spectral pigments and invisible nonspectral pigments gain more attention due to numerous applications in ecology, evolution, biomedical, and industrial perspectives. The international color symbolism chart indicates that each color has a specific meaning in different countries and cultures. Despite numerous known applications, evidence shows that visual pigments (color and light) can directly influence the brain [12], psychology [13], taste and flavor of humans [14][15][16], and science communication [17]. The lack of dietary pigments like carotenoids in our daily food intake may lead to various diseases and in rare case death [18]. Visual and food colorants are playing a significant role in decision making in our life to choose different foods and many other things [19], through vision, flavor, olfaction, gustation, and oral somatosensation ways [16].

Humans cannot see nonspectral colors due to a lack of trichromatic or tetrachromatic color vision-related cone types in their eyes. A recent study demonstrated humming birds' ability to perceive nonspectral colors via the tetrachromacy phenomenon [20]; another example of categorical color perception was observed in Estrildid finches [21]. Numerous studies have been exploring the spectral pigments from microbes and higher organisms for various

applications. Nevertheless, nonspectral pigments and their ecological importance in nature and biotechnological applications are not well studied. Thus, studies on nonspectral pigments remain a research gap in the current global science development scenario. Indeed, the planet earth is structured with visible and invisible micro and macromolecules produced by prokaryotes and eukaryotes, regulating various physical, chemical, biological, and geological processes. After going through a vast literature on microbial pigments, it is now understood that microbes and macro-organisms produce varied pigment molecules with a specific purpose in the respective milieus.

The resource of pigments, production rate, transport, price, sustainability, palatability, durability, effectiveness, legislative and regulatory approval, and demand by consumers are the primary requisites for various biotechnological applications in commercial industries. In this context, microbial pigments are attracting great demand to develop food grade, textile grade, and drug grade natural pigments. The reasons for high demand for microbial pigments are their promising unlimited resources, high production of required quantity of pigments, least cost-effective, easy cultivation and can be harvested throughout the year, adaptability to various environments, optimization, stability, genetic engineering, no side effects, eco-friendly, biodegradable, and indispensable applications in multidisciplinary aspects such as ecological, evolutionary, biomedical, agriculture, and industrial studies [9][22][23][24]. Many microbes are known to produce a wide variety of pigment molecules with innumerable biological properties and other industrial applications [9][25][26]. Especially, natural pigments of microbial origin have many advantages over synthetic pigments. Although artificial colors are more attractive and have been widely used around the world market (42%) [19][27][28][29][30], they are found to have many side effects (e.g., teratogenic, cancer, etc.) [29][30][31], and some are not biodegradable (e.g., textile dyes), causing health disorders to aquatic organisms and humans [32][33][34]. Hence, researchers are trying to find alternative physical, chemical, and biological methods to degrade synthetic colors [35][36][37] to avoid the side effects posed to the public and environmental health. Therefore, instead of developing synthetic colors and finding new methods for their degradation, exploring natural pigments from microbes would bring about innumerable advantages for the public and the environment.

2. Classification of Pigments

Microbes display all kinds of color hues such as black, blue, bronze, brown, cream, grey, green, orange, purple, indigo, pink, red, yellow, metallic green, red, yellow, and rainbow. These pigments can be classified into various categories based on their visual, chemical, and spectral properties and source of origin (based on mobile genes) [9]. Based on visual appearance, prokaryotes and eukaryotes display monochromatic to polychromatic pigment combinations within the Munsell color system. Some higher organisms like dragonfish [38][39] and hummingbirds [20] exceptionally display or see colors beyond our visible spectrum and near-infrared spectrum. These incidents suggest that humans lack nonspectral cones to perceive colors existing beyond the visible spectrum. Visually, pigments represent the following phenomena on earth: (1) Natural pigments, (2) Bioluminescence, (3) Fluorescence, and (4) Iridescence (structural colors), and (5) Non-spectral colors. Humans can perceive all the color phenomena except non-spectral colors.

Functionally, five different types of pigments are found in nature: (1) Biological pigments, (2) Fossil and sedimentary pigments, (3) Mineral pigments, (4) Synthetic & identical natural pigments, and (5) Caramel pigments (**Figure 1**). Biological pigments are derived from live microbes, plants, and animals. In contrast, fossil pigments are indeed biologically originated but preserved in fossils for millions of years, acting as evolutionary evidence [40][41][42][43][44][45]. In rare cases, fossil pigments can be of synthetic origin [46]. Mineral pigments are inorganic insoluble pigments used in artistic, cosmetic, archeological, and evolutionary studies [47][48][49][50][51][52]. In contrast, synthetic colorants are synthesized in the laboratory for food colorants and dyeing applications [53]. Dozens of synthetic colorants are being used in food and beverages [53][54]. Caramel pigments are natural sugar-based colorants used in a variety of food and beverage products. These caramel colors are classified into Caramel I, II, III, and IV classes to fulfill the requirement of food systems [55]. Solvatochromicity of these pigments varies according to the extraction solvent.

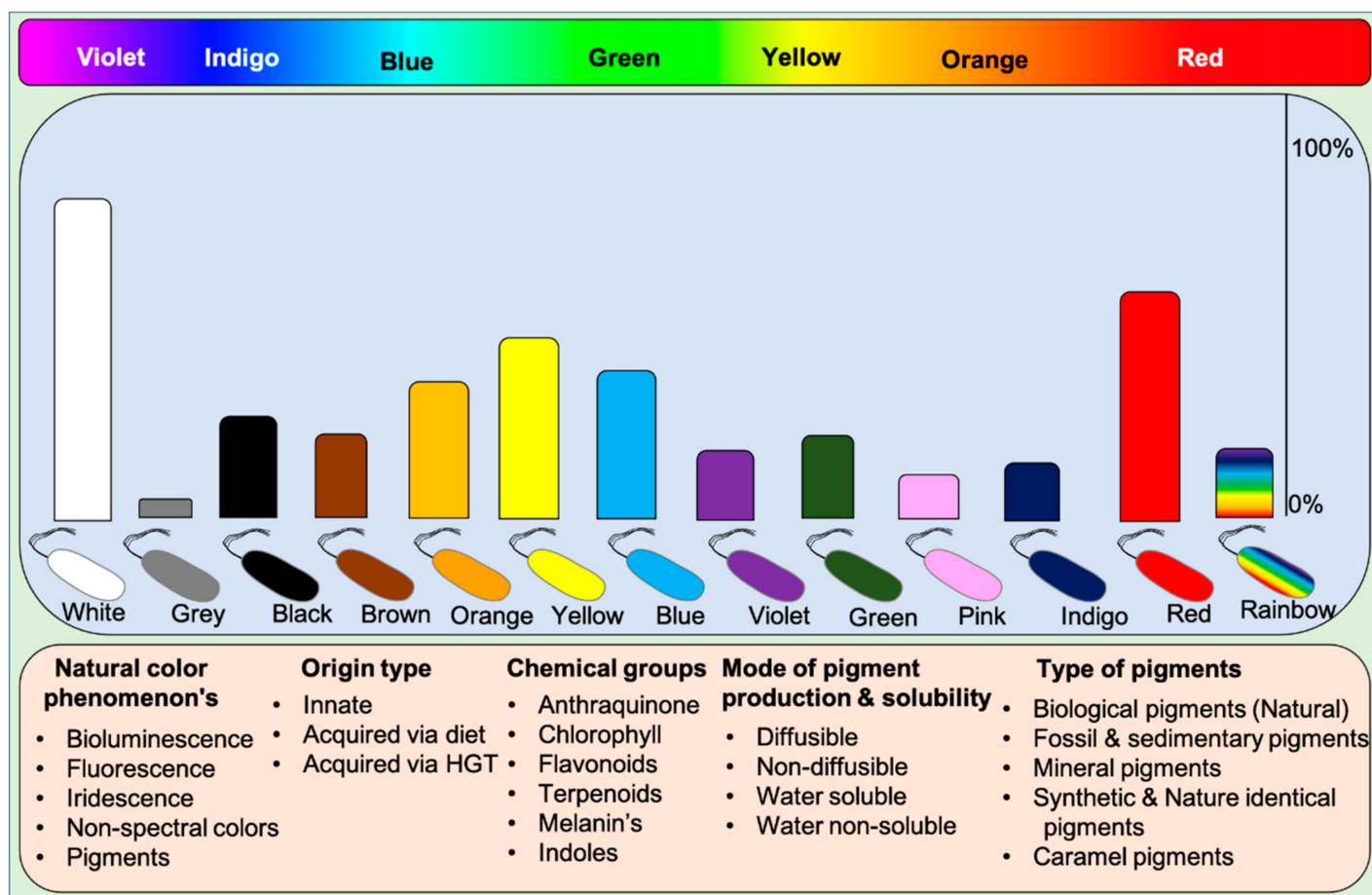


Figure 1. A wide array of pigmented microbes seen in nature. The abundance of the type of pigmented bacteria is depicted in bars based on the available literature. Rainbow bacteria are iridescent. Classification of pigments based on various aspects of biochromes. Chlorophyll pigments are not included in the data as they are ubiquitous. HGT: Horizontal gene transfer.

Based on chemical groups, microbial pigments are broadly differentiated into anthraquinones, carotenoids, indoles, phycobiliproteins, prodigiosin, rhodopsins, melanins, and violacein [9][56]. For understanding the evolutionary

aspects, rhodopsins, melanins, and iridescent (structural) pigments are briefly discussed herein. Microbial rhodopsins are light-harvesting photoproteins that bind to retinal and respond to light, which has evolutionary importance. These rhodopsin are found in Archaea, bacteria, fungi, viruses [57], and some eukaryotes [58]. Based on the known functions, rhodopsins are classified as light sensors (rhodopsins, opsins), energy-conserving transmembrane proton pumps (bacteriorhodopsins, proteorhodopsins, and xanthorhodopsins), and transmembrane chloride pumps (halorhodopsins) [4]. In Haloarchaea, a single cell can possess multiple rhodopsins with varied functions [4]. Melanins are biosynthetically, functionally, and structurally diverse pigments, including five known groups of allomelanin, eumelanin, and neuromelanin pheomelanin, and pyomelanin [59]. It is often easy to isolate monochromatic pigment-producing microorganisms from different environments, but isolation of polychromatic pigments producing bacteria such as *Pseudomonas aeruginosa* (blue and green pigments), *Streptomyces* sp. (yellow, orange and brown) [25] and iridescent or shimmering bacteria (VIBGYOR) [60] (<https://www.hoekmine.com>; accessed on 10 January 2021; Hoekmine BV, 2020) are rarely isolated. Structural colors are also recorded in fossil feathers, suggesting the importance of evolutionary aspects [61].

In general, microbes possess innate pigment traits, but some non-pigmented microbes acquire pigment traits from pigmented microbes (see the Section below: Horizontal Gene Transfer). For this reason, microbial pigments are classified as innate pigments and acquired pigments. Often, pigmented microbes release diffusible and non-diffusible pigments in culture media. However, rarely, some pigments are water-insoluble, for instance, blue pigment indigoidine [62], red pigment [63], and violacein [64]. Some pigments even do not dissolve in solvents; in such incidents, resin extraction can be employed to extract pigments.

3. Functions of Microbial Pigments

Microbial pigments are known to play a variety of ecological functions in their milieus. (Figure 2). Antioxidant properties of different microbial pigments are detailed in the supplementary file provided in the previous review published in 2019 (see supplementary file) [9]. Prodigiosin pigment produced by some strains of *Vibrio* sp. function as photoprotectants against UV light [65]. Violacein pigment of *Janthinobacterium lividum* and *Chromobacterium violaceum* demonstrated antipredator activity against bacterivorous nanoflagellates, indicating its defensive function [66]. *J. lividum* associated with the skins of some frogs and salamanders, secretes violacein pigment to protect them from pathogenic fungi, *Batrachochytrium dendrobatidis* [67][68][69]. Phenazine compounds produced by bacteria play multiple functions, including chemical signaling, biofilm formation, survival, and virulence [70]. Pyoverdine, a fluorescent yellow-green pigment, regulates iron transport and virulence functions in *Pseudomonas fluorescens* [71]. Tambjamine, a yellow pigment produced by *Pseudoalteromonas tunicata* [72], is suggested to help its host prevent other predatory fouling organisms [73]. Likewise, indigoidine, a blue pigment produced by *Phaeobacter* strains, is suggested to inhibit competing bacteria in the environment [74]. Bacterial melanin pigments act as photoprotectants [75][76][77][78][79]. For instance, *Vibrio cholerae* melanins serve as survival fitness factors when physico-chemical factors become unfavorable [80]. Some endophytic fungi releases anthraquinones, to protect the host plant from damage due to insects and microbes [81]; while, fungal melanins demonstrate multiple functions [82].

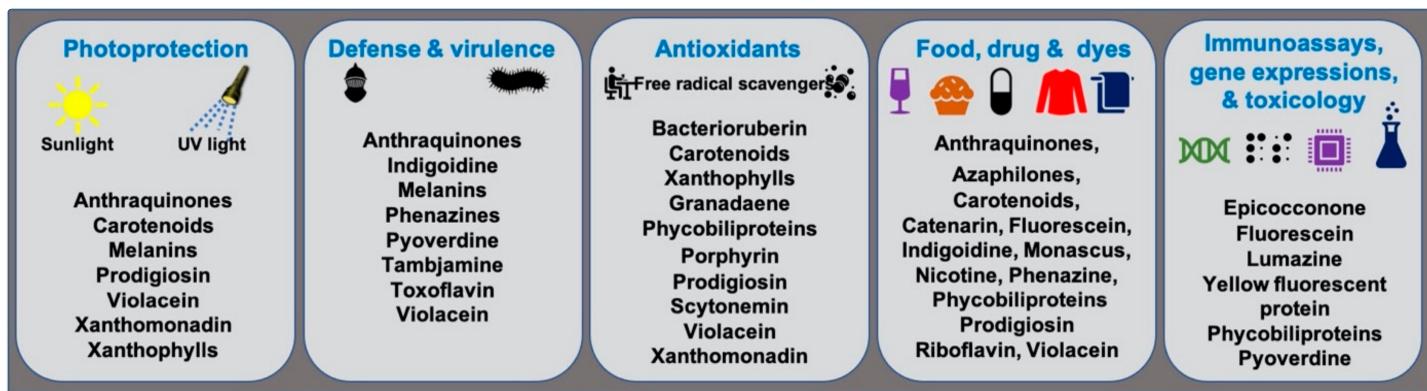


Figure 2. Ecological functions and other applications of important microbial pigments.

Bacteriochlorophylls are photosensitizers (light harvesters) in photosynthetic bacteria but absent in non-photosynthetic bacteria [83]. Non-photosynthetic bacteria may utilize a self-photosensitization mechanism [84]. In photosynthetic and non-photosynthetic bacteria, carotenoids, the accessory photosynthetic pigments act as photoprotectants and antioxidants, thus protecting cells from damage due to UV and sunlight illumination [83][85][86]. Bacterial communities in the air-water interface did produce more pigmentation to tolerate sunlight and are relatively drug-resistant compared to non-pigmented bacteria [87]. The extremophilic bacteria isolated from salt lakes [88] and cold environments like Antarctica [89][90] adopt environmental stress with carotenoids and other pigments. The yellow pigment of *Thermus* was proposed as a photoprotectant [91]. Carotenoids of archaea [92], yeasts [93][94], cyanobacteria, and algae [95] also function as photoprotectants. Marenine, a blue pigment produced by diatom *Haslea* is involved in greening on oysters [96], and displayed a prophylactic effect [97][98].

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