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Review

Natural Substrates and Culture Conditions to Produce Pigments from Potential Microbes in Submerged Fermentation

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Abstract: Pigments from bacteria, fungi, yeast, cyanobacteria, and microalgae have been gaining more demand in the food, leather, and textile industries due to their natural origin and effective bioactive functions. Mass production of microbial pigments using inexpensive and ecofriendly agro-industrial residues is gaining more demand in the current research due to their low cost, natural origin, waste utilization, and high pigment stimulating characteristics. A wide range of natural substrates has been employed in submerged fermentation as carbon and nitrogen sources to enhance the pigment production from these microorganisms to obtain the required quantity of pigments. Submerged fermentation is proven to yield more pigment when added with agro-waste residues. Hence, in this review, aspects of potential pigmented microbes such as diversity, natural substrates that stimulate more pigment production from bacteria, fungi, yeast, and a few microalgae under submerged culture conditions, pigment identification, and ecological functions are detailed for the benefit of industrial personnel, researchers, and other entrepreneurs to explore pigmented microbes for multifaceted applications. In addition, some important aspects of microbial pigments are covered herein to disseminate the knowledge.

Keywords: microbial pigments; submerged fermentation; natural substrates; antimicrobial and anticancer activities; dye and textile application; food colorants

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1. Introduction

The invisible microbial world comprises both non-pigmented and an array of pigmented microbes. They are visible to the human eye when cultured on agar plates. In the microbial world, numerous pigmented bacteria [1,2], fungi [3–6], yeast [7–10], cyanobacteria [11], and microalgae [12,13] have been identified. Pigment production in these organisms is mostly taxa or species specific, and their intracellular or extracellular pigments are extracted using traditional and green methodologies [14,15]. In general, these pigments are produced by microbes to tolerate environmental stress, for survival and competition [16]. Various microbial pigments of different chemical origins have demonstrated a wide range of applications [1,17,18]. Among the numerous known microbial pigments, prodigiosin [19–21], violacein [22], carotenoids [10,23–27], melanins [28,29], azaphilones [30,31], phycocyanin [32], phycoerythrobilin [33,34], and riboflavin [35] pigments have gained more demand in the global context as value-added products and medicine [23].

Although vast literature is available on plant pigments [36–38], microbial pigments are gaining more demand due to easy cultivation, large-scale production throughout the year, and biodegradability. Another reason for microbial pigment demand is the side effects

posed from synthetic colorants, such as hyperactivity disorder, cancer, allergies, and teratogenicity [39–41]. More significantly, synthetic dye effluents released from textile dyeing have been found to cause plant growth inhibition, air pollution, water contamination, and human illnesses [42]. Hence, many microbial pigments are used as food colorants [43]. The increasing demand for microbial pigments [2,44,45], mostly carotenoids, by various companies [10,23], is a sign of replacing the overuse of synthetic colorants in a wide range of applications.

The use of natural substrates to stimulate pigment production from microbes has become an important research approach in microbial biotechnology. A variety of agro-waste substrates and other natural substrates have been tested against different microbes in submerged fermentation [10,45–48]. In view of the importance of such substrates in pigment production, the search for new agro-waste substrates is still being continued globally by researchers [45]. On the other hand, the search for novel pigment genes with potential dyeing, cosmetic, drug, and food colorant applications is underway across the world, including from polar regions to deep-sea hydrothermal vents [45,49]. Large-scale screening of pigmented microbes from different environmental setups would not only unveil novel genes with different biosynthetic pathways but also delineate the evolutionary origins of pigmented microbes. Therefore, in a special way, this review is a treatise to benefit researchers and industrial personnel.

2. Pigmented Microbial Distribution in Evolutionary Perspective

A wide array of pigmented microbes are known to be distributed across The North Pole to The South Pole and from the Eastern to Western hemisphere [1,45]. Pigmented microbes such as bacteria, fungi, yeast, and microalgae are identified from a wide range of environments, such as marine [50,51], freshwater [16], desert [52], cryosphere [49], soil setups [1,53], and space [54] (Table 1). Their occurrence in various environments has been linked to evolutionary studies [45]. For instance, a recent review shows the distribution of prodigiosin and violacein pigment-producing bacteria from terrestrial and marine environments [45]. Similarly, *Monascus*-like pigments belonging to the azaphilone chemical class have been identified from ascomycetous fungi that originated from marine and terrestrial habitats [55,56]. These reports suggest that many other lesser known or unexplored microbial pigment molecules (across the microbial taxa) might have a specific evolutionary origin, relationships, and spread in different environments. The occurrence of pigmented bacteria in wastewaters [57,58] also indicates their function in a specific environmental setup. Therefore, exploration of novel microbial pigments, their molecular phylogeny, and chemicalomics investigations from extreme environments such as hydrothermal vents, cold springs, and glaciers are needed to shed light on evolutionary origins and their convergent and divergent pathways.

Table 1. Few examples of industrially important pigmented microbes isolated from various environments and their applications.

Pigmented Microbe	Pigment	Source	Application	Reference
Bacteria				
Bacillus	Carotenoid	Different sources	Colorant	[59]
Chromobacterium violaceum	Violacein	River water and agricultural waste	Antimicrobial	[22]
Janthinobacterium sp.	Violacein	River water	Antimicrobial	[16]
Paracoccus carotinifaciens	Astaxanthin	Soil	Coloring agent	[60]
Planococcus sp.	Carotenoid	Wastewater	Food additive	[57]
Serratia marcescens	Prodigiosin	Soil	Dye, antimicrobial	[61]
Streptomyces cavourensis	Melanin	Sea cucumber	Antimicrobial	[62]

Table 1. *Cont.*

Pigmented Microbe	Pigment	Source	Application	Reference
Bacteria				
Streptomyces sp.	4,8,13-trihydroxy-6,11-dione-trihydrogranaticins A (TDTA)	Soil	Feed additive	[63]
Fungi				
Monascus purpureus	*Monascus* red pigment	Red mold rice	Food colorant	[64]
Monascus ruber	*Monascus* red pigment	Soil	Food colorant	[65]
Talaromyces albobiverticillius	*Monascus*-like	Marine	Industrial	[56]
Yeast				
Rhodotorula glutinis	Carotenoid	Soil	Food colorant	[66]
Rhodotorula paludigena	Carotenoid	Mangrove	Fish feed	[67]
Xanthophyllomyces dendrorhous (=*Phaffia rhodozyma*)	Astaxanthin	Trees	Food additive	[68,69]
Cyanobacteria				
Arthrospira maxima (=*Spirulina maxima*)	Phycocyanin	Freshwater	Food and drug	[70]
Arthrospira platensis (=*Spirulina platensis*)	Phycocyanin	Freshwater	Dye and food additive, fluorescent probe	[71,72]
Arthrospira platensis	Phycocyanin	Seawater	Food and drug	[73]
Microalgae				
Chlorella vulgaris	Carotenoids	Freshwater	Food and drug	[74]
Cyanidioschyzon merolae	Phycocyanin	Hot sulfuric springs and geysers	Food colorant	[75]
Cyanidium caldarium	Phycocyanin	Thermal area	Food colorant	[76]
Cyanophora paradoxa, *Dunaliella salina*	Zeaxanthin and β-cryptoxanthin	Freshwater	Anticancer	[77]
Galdieria sulphuraria	Phycocyanin	Hot and acidic springs	Food and drug	[78]
Haematococcus pluvialis	Astaxanthin	Freshwater	Feed additive	[79]
Haslea ostrearia	Marennine	Seawater	Food colorant and drug	[80,81]
Phaeodactylum tricornutum	Fucoxanthin	Marine	Anti-inflammatory	[82]

3. Important Pigments for Submerged Fermentation

Not many pigmented microbes are reported to have food and drug applications due to some of the following reasons: (1) they are unable to grow on culture media after one or more subcultures, (2) difficulty in storing cultures alive, unlike non-pigmented microbial cultures, (3) low pigment yield, (4) inability/loss of pigment-producing nature under stress, (5) low or no bioactivity, (6) lack of dyeing and food colorant application, (7) unstable properties at various physicochemical factors, and (8) pathogenicity and toxins associated with some microbes [1]. Hence, these points need to be reckoned while screening pigments for various applications to save time and chemicals and reagents (for more details on this aspect, see Sections 7 and 8 below). The literature clearly indicates that violacein, prodigiosin from bacteria [19], azaphilones from fungi [30], and carotenoids from yeast [10] and microalgae [83] are the major pigments extensively studied in submerged fermentation for industrial applications (Figure 1). The use of these microbial dyes is highly regulated by legislation, which varies from country to country. For example, azaphilones from *Monascus* have been used in Asia for centuries but are still forbidden in Europe and the

USA. In Europe, β-carotene and lycopene from the filamentous fungus *Blakeslea trispora* are now in current use, and safety authorities concluded that α-tocopherol-containing oil suspension of the carotenoids β-carotene or lycopene, obtained from *B. trispora*, for use as an ingredient in feedstuffs or foodstuffs is not of concern from a safety point of view. There are also huge health safety issues with synthetic food colorants, and in a few years a list of safe, natural colorants coming from many sources (plants, microalgae, fungi, yeasts, bacteria) will emerge. In addition, the pigment production rate of microbes in submerged fermentation in the presence of various agro-industrial supplements gives a decision-making stage where a particular pigmented microbe is selected or not for further studies. Thus, currently, microbes with novel pigments, more bioactivity, and high pigment yield are explored by global researchers.

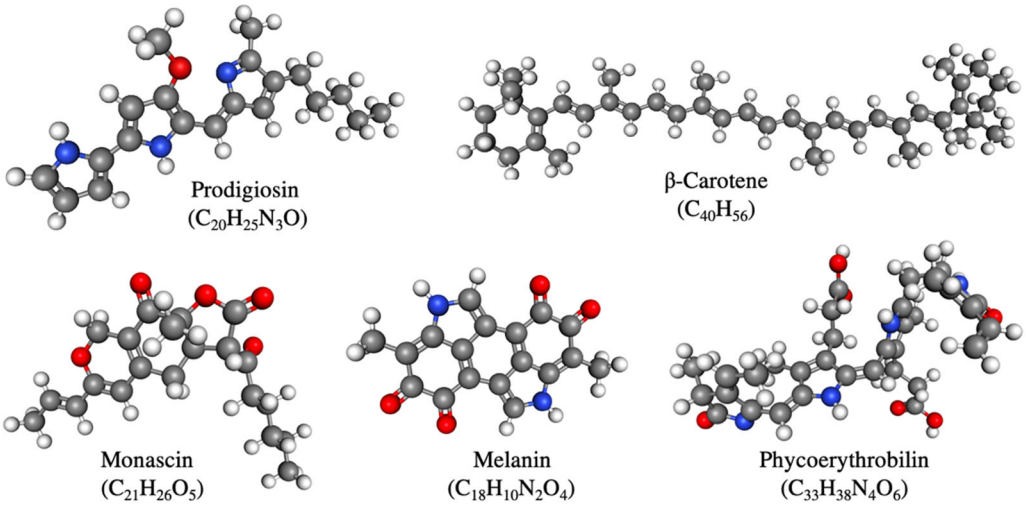

Figure 1. The 3D chemical structures of industrially important microbial pigments. Images are drawn in MolView online program (https://molview.org/, accessed on 4 July 2022).

4. Biosynthetic Pathways of Major Microbial Pigments

Understanding the biosynthetic pathways of pigments is a key step to make required alterations in the pigment gene clusters and enhance the pigment yield. A variety of pigment gene cassettes found in different microbes were reviewed previously [84] and recently [45]. The biosynthetic pathways of violacein [22] and prodigiosin [20,85] have been well understood. Likewise, the biosynthetic pathways of different classes of bacterial and fungal melanins are well understood and used in a variety of applications [28]. Carotenoid biosynthesizing genes are widely investigated from several fungal species [3], yeast, *Xanthophyllomyces dendrorhous* [86], and microalgae [87], due to their importance in value-added food products. Scytonemin, a cyanobacterial pigment with cosmetic and drug value, was well studied, and its biosynthetic gene clusters (*scy*, *trp*, *ebo*) were identified [88].

For researchers involved in experiments about microbial pigments, biosynthetic pathways have always been the core knowledge to be described as a priority. More than 30 years ago, there existed no high-throughput sequencing, synthetic biology, nor genomics, but progress was made on microbial biosynthesis of carotenoids [89]. The enzymes and genes which mediate the biosynthesis of carotenoids such as lycopene, isorenieratene, β-carotene, and phytoene were unknown up to 1990, when Misawa et al. [89] elucidated for the first time the pathway for biosynthesis of β-carotene at the level of enzyme-catalyzed reactions, using bacterial carotenoid biosynthesis genes (expression of *Erwinia uredovora* genes in the host *Escherichia coli*). Hundreds of papers are now available regarding the biosynthesis of carotenoids in microorganisms, and thousands of carotenogenic biosynthetic genes are available in databases. However, knowing the genes is not enough to obtain a large expression of these genes in the original organism or in a host [90]. Most of the current research is now dedicated to the identification of the metabolic bottleneck(s) that make(s) it

impossible to obtain commercial productions of microbial pigments. Substrate inhibition of enzymes can be a major drawback for the efficient production of valuable biochemicals in engineered microorganisms. In a recent study, Ma et al. (2022) showed that substrate inhibition of lycopene cyclase was the main limitation in carotenoid biosynthesis in the yeast *Yarrowia lipolytica* [91] and, after some genetic modifications, were able to reach 39.5 g/L β-carotene in the fermenter (a 1441-fold enhancement related to the original strain). Such advances now allow microbial pigments to outperform pigments of plant origin or from chemical synthesis.

The second example showing the crucial importance of the biosynthetic pathway studies deals with *Monascus* azaphilone pigments (MAPs), which are the fermentation products of the filamentous fungi *Monascus* spp. These MAPs are widely used in the food industry as pigments, colorants, and dyes. Despite their widespread use, efficient production of MAPs still has some challenges to address, such as the reduction in hepatotoxic mycotoxin citrinin and anti-hypercholesterolemia agent monacolin K contaminations, which are unwanted compounds in the food ingredient industry. Liu et al. (2022) sequenced the genomes of twenty-six *Monascus* species and proposed a novel classification system, consisting of sections A, B, and C, according to the biosynthetic gene cluster (BGC) distributions and phylogeny results [92]. Based on the absence of citrinin biosynthetic genes, section B species should be investigated in the near future. The biosynthesis of *Monascus* pigments has been studied for decades, and this recent publication proves that more work is still needed, as it is also requested for all classes of microbial pigments.

The third example is also about a pigment not produced by plants, specific to some microorganisms. Violacein pigment synthesis in Gram-negative bacteria is encoded by five enzymes and formed by tryptophan. Xu et al. (2022) newly discovered violacein operon *vioABCDE* in the genome of the extremophile *Janthinobacterium* sp. B9-8 [93]. Cloning of *Janthinobacterium* heterologous genes into engineered *Escherichia coli* resulted in violacein production up to 107 mg/L in a two-stage fermentation process compared to the original strain.

The last example we wanted to develop describes how microorganisms can be used to produce pigments produced only by plants up to now. Anthocyanins are phenolic molecules that give color to fruits and vegetables. Anthocyanins bring many health benefits to humans [94]. Research about anthocyanin biosynthesis regulation in heterologous hosts is currently attracting the interest of many researchers. For improving the production of microbial anthocyanins and to increase the commercial competitiveness of the microbial production, problems and questions such as low expression of genes and inappropriate balancing of genes involved in the microbial biosynthetic pathways of anthocyanins should be answered [95]. Following these steps, anthocyanin production through bacteria, yeast, and fungi will soon be a new success of microbial pigment science.

5. High Pigment Yielding Natural Substrates

The concentration (intensity) of microbial pigments usually varies according to species and strain. In the laboratory conditions, some pigmented microbes produce high-quantity and high-concentration pigments, while some produce low-quantity and low-intensity pigments. The use of a variety of natural/synthetic substrates to stimulate and enhance the yield of microbial pigments has been reviewed, and indicated natural substrates as a potential nutrient element in microbial pigment production [45]. Thus, the use of genetic engineering modification techniques, which are costly and time consuming, have limitations but remain an option to improve strains. However, it is not an essential step to improve pigment production unless the strain has proven to have specific bioactivity or coloring applications. In exceptional cases, mutagenesis and genetic engineering techniques are implemented for strain improvement as well as to enhance pigment production from a low pigment yielding microbe with potential application [96].

The use of natural substrates and adsorbents [45] in fermentation plays an important role in enhancing cell volume during frothing. Several studies have demonstrated

the application of natural substrates on the yield of various microbial pigments due to the presence of rich carbon–nitrogen residues [48]. However, only some substrates are demonstrated to yield more pigment [10,45–48]. Several studies have investigated a large number of agro-industrial substrates in solid-state fermentation compared to submerged fermentation [97]. Here, substrates with high pigment yielding ability used in submerged fermentation are alone detailed briefly for further implications (Table 2).

Higher prodigiosin production from *S. marcescens* was achieved using peanut broth (38.75 mg mL^{-1}) than other substrates [61]. For more substrates with a good yield of prodigiosin pigment, refer to Han et al. (2021) [20]. Among the several tested substrates, prodigiosin pigment production was enhanced greatly with cassava wastewater [98] and peanut oil cake [99].

Monascus purpureus culture produced more pigment yield when tested with corncob hydrolysate [100], bakery waste hydrolysate [101], brewer's spent grain [102], and glucose fermentation medium added with rice straw hydrolysate [103] (Table 2). *Monascus ruber* produced significantly low pigment yield when supplemented with sugarcane bagasse hydrolysate [104] (Table 2). The waste extract medium made up of various peels of inedible fruit matter was reported to enhance carotenoid production from several species of *Rhodosporidium*, especially from *Rhodosporidium toruloides* [105]. Many agro-industrial residues tested were found to enhance carotenoid production from several yeast species [10,45]. Loquat kernel extract [66], sugar beet molasses [106], and sugar cane extracts [107] were the two substrates reported to enhance yeast carotenoids greatly.

Table 2. Various substrates stimulating high pigment content from industrially important microbes. Readers may refer to the corresponding references for more details about the substrate concentration and media composition.

Pigment Microbe	Species	Substrate	Pigment	Production Rate	Method	Reference
Bacteria	*Bacillus safensis*	Fruit waste of pineapple, orange, and pomegranate	Melanin	6.96 mg/mL	Shake flask	[108]
	Bacillus subtilis	Corn steep liquor	Riboflavin	26.8 mg/L	Shake flask	[109]
	Chromobacterium vaccinii	Rapeseed cake	Violacein	12.93 mg/L	Shake flask	[110]
	Chromobacterium violaceum	Liquid pineapple waste	Violacein	16.25 mg/mL	1 L Bioreactor	[111]
	Chromobacterium violaceum	Sugarcane bagasse	Violacein	820 mg/L	Shake flask	[112]
	Chryseobacterium artocarpi	Liquid pineapple waste	Flexirubin	540 mg/L	Shake flask	[113]
	Pseudomonas sp.	Vegetable waste	Melanin	2.79 mg/mL	Shake flask	[114]
	Pseudomonas aeruginosa	Cotton seed meal	Pyocyanin	4 µg/mL	Shake flask	[115]
	Pseudomonas aeruginosa	Grape seed	Pyocyanin	4 µg/mL	Shake flask	[115]
	Sarcina sp.	Apple pomace	Carotenoid	12.87 mg/100g	Shake flask	[116]
	Serratia marcescens	Cassava wastewater	Prodigiosin	49,500 mg/L	Shake flask	[98]
	Serratia marcescens	Peanut oil cake	Prodigiosin	40,000 mg/L	Shake flask	[99]
	Serratia marcescens	Tannery fleshing	Prodigiosin	33,000 mg/L	Shake flask	[117]
	Serratia marcescens	Peanut seed broth	Prodigiosin	38.75 mg/mL	Shake flask	[61]
	Serratia marcescens	Peanut seed oil	Prodigiosin	0.02 gm/mL	Shake flask	[118]
	Serratia marcescens	Brown sugar	Prodigiosin	8 mg/mL	5 L Bioreactor	[119]
	Serratia marcescens	Peanut powder and olive oil	Prodigiosin	15,420.9 mg/L	Shake flask	[120]
	Serratia marcescens	Powdered peanut	Prodigiosin	1595.09 mg/L	Shake flask	[121]
	Serratia marcescens	Wheat bran and sunflower oil	Prodigiosin	240 mg/L	Shake flask	[122]

Table 2. *Cont.*

Pigment Microbe	Species	Substrate	Pigment	Production Rate	Method	Reference
Fungi	*Serratia marcescens*	Powdered peanut	Prodigiosin	39 mg/mL	Shake flask	[61]
	Serratia marcescens	Sesame seed	Prodigiosin	17 mg/mL	Shake flask	[61]
	Streptomyces sp.	Dairy processing wastewater	Prodigiosin	47,000 mg/L	Shake flask	[123]
	Aspergillus carbonarius	Apple, black carrot, pomegranate, red beet pulps	Melanin	61.84 U/gm	Shake flask	[124]
	Blakeslea trispora	Cheese whey	Carotenoid	405 mg/L	1.4 L glass bioreactor	[125]
	Eremothecium gossypii(=*Ashbya gossypii*)	Corn steep liquor	Riboflavin	13.7 gm/L	Shake flask	[126]
	Monascus purpureus	Rice husk hydrolysate	*Monascus*	72.1 U/mL	Shake flask	[127]
	Monascus purpureus	Potato pomace	*Monascus*	47.9 U/mL	Shake flask	[64]
	Monascus purpureus	Whey powder	*Monascus*	38.4 U/mL	Shake flask	[128]
	Monascus purpureus	Corncob hydrolysate	*Monascus*	25.80 U/mL	Shake flask	[100]
	Monascus purpureus	Corncob	*Monascus*	133.77 U/mL	Shake flask	[129]
	Monascus purpureus	Bakery waste hydrolysate	*Monascus*	24.01 U/mL	Shake flask	[101]
	Monascus purpureus	Brewer's spent grain	*Monascus*	22.25 U/mL	Shake flask	[102]
	Monascus purpureus	Soybean meal	*Monascus*	21.45 U/mL	Shake flask	[46]
	Monascus purpureus	Rice straw hydrolysate with glucose	*Monascus*	21.20 U/mL	Shake flask	[103]
	Monascus purpureus	Grape waste	*Monascus*	20–22.5 gm/L	Shake flask	[130]
	Monascus ruber	Sugarcane bagasse hydrolysate	*Monascus*	18.71 U/mL	Shake flask	[104]
	Penicillium purpurogenum	Orange peels	*Monascus*-like	0.58 U/mL	Shake flask	[131]
	Sporidiobolus pararoseus	Corn steep liquor	Carotenoid	40 gm/L	Shake flask	[132]
	Talaromyces atroroseus	Corncob hydrolysate	*Monascus*	16.17 U/mL	Shake flask	[133]
	Talaromyces purpureogenus	Bengal gram husk	*Monascus*	0.565 U/mL	Shake flask	[134]
Yeast	*Rhodotorula achenorium*	Whey ultrafiltrate	Carotenoid	262 mg/L	Shake flask	[135]
	Rhodotorula glutinis	Brewery wastewater	Carotenoid	1.2 mg/L	Shake flask	[136]
	Rhodotorula glutinis	Mung bean waste flour and sweet potato extract	Carotenoid	3.48 mg/L	Shake flask	[137]
	Rhodotorula glutinis	Cassava wastewater	Carotenoid	0.98 mg/L	Shake flask	[138]
	Rhodotorula glutinis	Crude glycerol	Carotenoid	135.25 mg/L	Shake flask	[139]
	Rhodotorula glutinis	Chicken feathers	Carotenoid	92 mg/L	Shake flask	[140]
	Rhodotorula glutinis	Whey	Carotenoid	46 mg/L	Shake flask	[141]
	Rhodotorula rubra	Sugarcane juice	Carotenoid	30.39 mg/g	Shake flask	[107]
	Rhodotorula rubra	Whey ultrafiltrate	Carotenoid	12.1 mg/L	Shake flask	[142]
	Rhodotorula rubra	Whey sugar	Carotenoid	0.705 OD/ml	Shake flask	[143]
	Rhodosporidium mucilaginosa	Potato extract	Carotenoid	56 mg/L	Shake flask	[141]
	Rhodosporidium mucilaginosa	Coffee husk extract	Carotenoid	21.35 mg/L	Shake flask	[144]
	Rhodosporidium mucilaginosa	Coffee pulp extract	Carotenoid	16.36 mg/L	Shake flask	[144]
	Rhodosporidium mucilaginosa	Cassava bagasse	Carotenoid	12.5 mg/L	Shake flask	[145]
	Rhodosporidium mucilaginosa	Onion peels and mung bean husk	Carotenoid	719.69 µg/g	Shake flask	[146]

Table 2. *Cont.*

Pigment Microbe	Species	Substrate	Pigment	Production Rate	Method	Reference
	Rhodosporidium toruloides	Waste extract	Carotenoid	62 mg/L	Shake flask	[105]
	Rhodosporidium toruloides	Wheat straw hydrolysate	Carotenoid	24.58 mg/L	Shake flask	[147]
	Rhodosporidium toruloides	Carob pulp syrup	Carotenoid	9.79 µg/L	Shake flask	[148]
	Rhodotorula glutinis	Loquat kernel extract	Carotenoid	62.73–72.36 mg/L	Shake flask	[66]
	Rhodotorula glutinis	Waste chicken feathers	Carotenoid	6.47 mg/g	Shake flask	[140]
	Sporodiobolus pararoseus	Corn steep liquor and parboiled rice water	Carotenoid	0.84 mg/L	Shake flask	[132]
	Sporodiobolus pararoseus	Sugarcane molasses and corn steep liquor	Carotenoid	0.52 mg/L	Shake flask	[149]
	Sporidiobolus salmonicolor	Corn maceration and rice parboiling water	Carotenoid	7.38 mg/L	2 L Bioreactor	[150]
	Sporidiobolus salmonicolor	Cheese whey hydrolysate	Carotenoid	590.4 µg/L	Shake flask	[151]
	Sporidiobolus pararoseus	Corn steep liquor and par- boiled rice water	Carotenoid	843 µg/L	Shake flask	[132]
	Xanthophyllomyces dendrorhous	Sugar beet molasses	Astaxanthin	40 mg/L	100 L Bioreactor	[106]
	Xanthophyllomyces dendrorhous	Eucalyptus hydrolysate	Astaxanthin	30.5 mg/L	2 L Bioreactor	[152]
	Xanthophyllomyces dendrorhous	Mustard waste	Astaxanthin	25.8 mg/L	Shake flask	[153]
	Xanthophyllomyces dendrorhous	Date juice	Astaxanthin	23.8 mg/L	3 L Bioreactor	[154]
	Xanthophyllomyces dendrorhous	Molasses	Astaxanthin	15.3 mg/L	Shake flask	[155]
	Xanthophyllomyces dendrorhous	Grape juice	Astaxanthin	9.8 µg/mL	Shake flask	[156]
	Xanthophyllomyces dendrorhous	Mesquite pods and corn steep liquor	Carotenoid	293.41 ± 31.12 µg/g	Shake flask	[157]
Microalgae	*Haematococcus pluvialis*	Primary-treated piggery wastewater	Astaxanthin	83.9 mg/L	Shake flask	[79]
	Phormidium autumnale	Slaughterhouse wastewater	Carotenoid	107,902.5 kg/year	2 L Bioreactor	[158]

6. Submerged Culture Conditions for Pigment Production

Usually, pigmented bacteria, fungi, and yeast are highly sensitive to physicochemical parameters. Thus, these microbes require a variety of in vitro culture conditions to yield more pigments in either solid-state or submerged fermentation. It is necessary to investigate the optimized culture conditions for each species or strain. Therefore, optimization of experimental design studies using artificial neural networks, Box–Behnken design, central composite design, Plackett–Burman design, and response surface modeling have been used to identify the key physicochemical factors that trigger high pigment production in microbes. Regardless of species, a review of the literature suggests that most pigmented microbes, except few cases, produce pigments at temperatures ranging between 22–28 °C, pH 5–6, and agitation at 100–150 rpm [1,10] (Table 3).

The maximum prodigiosin pigment production from *S. marcescens* was observed at 28 °C (38.75 mg/mL) compared to 30 °C (25.98 mg/mL) when cultured in peanut seed broth but not with other substrates tested [61]. Many species of fungi and yeast were

observed to produce carotenoid pigments under various parameters such as temperature, pH, agitation, and light availability [10]. *Monascus purpureus*, when cultured with whey powder [128], bakery waste hydrolysate [101], and corncob hydrolysate [100], was able to produce more pigments at 30 °C. Numerous yeast species have been observed to yield more carotenoid pigments at pH 5 and temperature below 30 °C [10]. On the other hand, carotenoid production from microalgae *Haematococcus pluvialis* and *Phormidium autumnale* have demonstrated the maximum yield at 23 °C [79] and 26 °C [158], respectively. The pigment yield levels from microbes depends on the type of substrate used in submerged fermentation (Table 3).

Table 3. Culture conditions set along with various agro-waste to produce different microbial pigments in submerged fermentation. Readers may refer to the respective reference for more details about the concentration of each substrate used in submerged fermentation.

Pigment	Substrate	Temperature	pH	Reference
Carotenoid	Wheat straw hydrolysate	30 °C	5.3	[147]
	Coffee husk media	28 °C	5.7	[144]
	Corn maceration and rice parboiling water	25 °C	4.0	[150]
	Cassava bagasse	25 °C	6.0	[145]
	Corn steep liquor and parboiled rice water	25 °C	4.0	[132]
	Rice powder	35 °C	7.0	[159]
	Mesquite pods and corn steep liquor	20 °C	5.5	[157]
	Cheese whey	26 °C	7.3	[125]
	Primary-treated piggery wastewater	23 °C	7.5	[79]
	Slaughterhouse wastewater	26 °C	7.6	[158]
Flexirubin	Liquid pineapple waste	30 °C	7.0	[113]
	Fruit pulp	25 °C	6.5	[124]
Melanin	Fruit waste	30.7 °C	6.8	[108]
	Vegetable waste	25 °C	7.0	[114]
	Potato pomace	28 °C	5.0	[64]
Monascus	Glucose fermentation media	30 °C	5.5	[103]
	Whey medium	30 °C	6.0	[128]
	Grape waste	30 °C	6.5	[46]
	Brewer's spent grain media	30 °C	5.5–7.5	[102]
Monascus-like	Rice powder	32 °C	3.5	[160]
	Potato dextrose broth	24 °C	6.4	[161]
	Orange peels	24 °C	5.0	[131]
	Brown sugar	25 °C	7.0	[119]
	Cassava wastewater	28 °C	7.0	[98]
Prodigiosin	Peanut oil	28 °C	-	[118]
	Peanut powder and olive oil	26 °C	7.0	[120]
	Powdered peanut broth	28 °C	7.0	[61]
	Peanut oil cake	30 °C	7.0	[99]
Pyocyanin	Wheat bran medium	30 °C	-	[122]
	Cotton seed meal media	37 °C	-	[115]
Riboflavin	Corn steep liquor	37 °C	7.2	[109]
	Corn steep liquor	28 °C	6.8	[126]
Violacein	Liquid pineapple waste	30 °C	7.0	[111]
	Sugarcane bagasse	30 °C	7.0	[112]

7. Rapid Identification of Microbial Pigments

The identification of pigments from microbes is easier compared to non-pigmented microbial compounds. Identification of non-pigmented compounds on thin-layer chromatography (TLC) requires additional tests and UV visualization. However, rapid extraction, purification, and identification of pigments has become easy due to color appearance. For

instance, the TLC technique, a simple and cost-effective method, was quick and effective to purify and identify red pigments [162] (Figure 2). TLC is a cheaper technique compared to other chromatographic techniques such as high-performance liquid chromatography (HPLC) and high-performance thin-layer chromatography (HPTLC), which are basically costly instruments that require more maintenance and costly consumables to process samples. Hence, TLC outstands as the cheapest and most efficient method to purify pigments. It is not clear whether or not pigmented microbes display cellular vitiligo (a condition in which the bacterial cell wall may display patchy loss of pigmentation) condition. However, it is easier to purify extracted pigments (intra- and extracellular) of any microbe using TLC. Some wild fungal species and some cultured species on agar plates release droplets of concentrated pigmented molecules on their filaments' surface. These compounds are collected using a syringe (Figure 3) and mixed (authors' unpublished data) in methanol (because methanol has high polarity and better extractive yield) to test their bioactivity and colorant properties. It is not possible to obtain enough quantity of pigment droplets to test a large number of cytotoxicity and antimicrobial assays using this approach. Thus, this approach serves as a simple and rapid technique to determine the bioactive nature of pigment droplets using fewer bioassays. Thereby, this rapid method allows researchers to decide whether or not to choose a pigmented microbe that releases pigment droplets for submerged fermentation. Upon confirming the biological properties, pigment droplets can be purified easily using TLC, as shown in Figure 2. After obtaining clear, distinct pigment bands with TLC;TLC plates are allowed to dry at room temperature to evaporate the solvents on the silica gel. Then those bands are scraped using sterile pointed blades, and the eluted pigments are collected in a micro-vial to identify the pigments using HPLC, Fourier-transform infrared spectroscopy (FT-IR), liquid chromatography–mass spectrometry (LC-MS), and nuclear magnetic resonance (NMR) analyses.

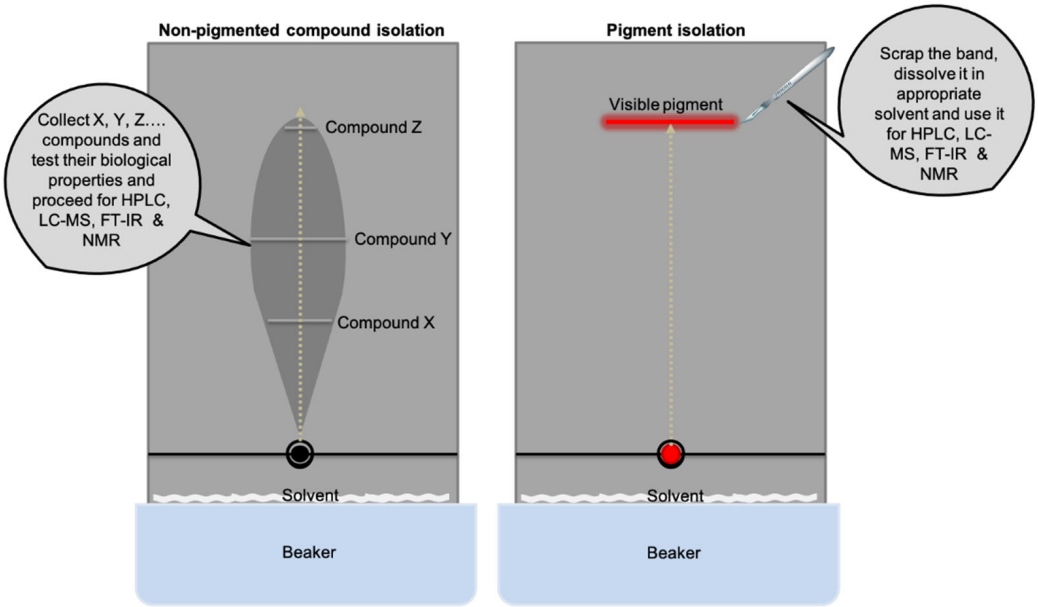

Figure 2. Illustration depicting the TLC technique as the easiest, rapid, effective, cheap, and time saving method to isolate and purify pigment molecules over non-pigmented compounds.

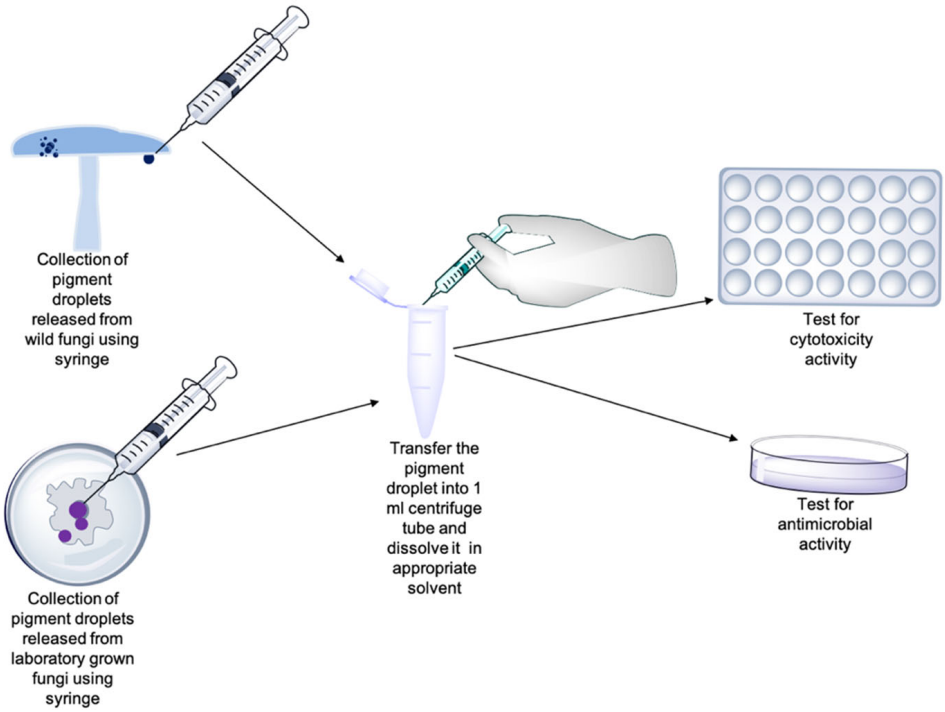

Figure 3. Isolation of concentrated pigment droplets (authors' unpublished data) released by fungi on their mycelia surfaces and testing them directly for biological properties in a simple and rapid way. Before or after confirming the bioactivity, these pigment droplets can be purified with TLC as shown in Figure 2.

8. Need for Targeted Drug Research on Microbial Pigments

Numerous studies have widely studied the potential biological properties of microbial pigments as antimicrobial and anticancer agents. The antimicrobial activities of microbial pigments against common pathogens and/or using strains that are available in their laboratory have been reported very often. However, the current research need is to find the molecules that combat multidrug-resistant microbes (MDRM) and a variety of cancer cells. Therefore, a routine antimicrobial investigation using pathogens (which are not of current interest) may be useful only for documentation but not in drug development research if considering the following reasons: (1) to find an effective pigment molecule against targeted MDRM and currently emerging pathogens, and (2) to develop a potential anticancer pigment molecule. Research work merely focusing on routine antibacterial properties for documentation and publications may no longer support the rapid development of drugs and help public health. Therefore, it is urgent to realize that the targeted research on the above two points using microbial pigments is very important to save time, research budgets, and hard work. In addition, one of the important notes is finding effective pigment molecules for rapid development of food colorant drug applications without repeating or duplicating the works performed before. The literature review has indicated the photodynamic photopigment therapy (i.e., the activation of photosensitizing pigments by light energy to treat a variety of diseases and infections) as an effective method to treat cancer and several microbial infections [45,163]. Therefore, studies that deal with microbial pigments need to perform photopigment therapy based on antimicrobial and other biological properties to understand the bioactive nature of microbial pigments in the presence and absence of light treatments.

Furthermore, the use of animal models in in vivo studies has constraints such as finance and ethics. In this regard, *Galleria mellonella* has been identified as a widely used, cheaper, and alternative model to study the cytotoxicity effect of a candidate drug. This invertebrate model requires no ethical approvals, is significantly cheaper, and its short lifespan enables it to be an ideal invertebrate model for high-throughput research [164].

The response of *G. mellonella*, which shares some similarities with the mammalian innate immune system, is the most crucial feature that makes it a useful preclinical in vivo model [165–167]. In comparison to mammals, this mini-host has economic and ethical benefits, and its short lifespan makes it an ideal model for high-throughput investigations of a variety of compounds [168,169]. They can readily be cultivated at 37°C in an incubator, giving researchers more control over the experimental situation and allowing them to examine clinically relevant human pathogens at a temperature similar to the human host, resulting in precise and reliable data [170]. Therefore, alternative invertebrate models such as *G. mellonella* larva may be used as an effective and rapid preclinical in vivo model to determine the cytotoxicity of pigments.

9. Role of Pigmented Microbes in Climate Change

The global temperature has been increasing in recent years due to anthropogenic gases released from industrialization, automobiles, and the enormous use of greenhouse-gas-releasing systems [171]. Therefore, the current research trend has turned towards green energy, green chemistry, and green earth concepts. The toxic gases and water discharges released from the synthetic colorant manufacturing industries and textile industries using synthetic colorants are entering the atmosphere [39,42,172]. Therefore, the use of microbial pigments over synthetic colorants would eliminate toxic gases and other pollutants emitted from parties manufacturing and utilizing synthetic colorants. Therefore, efforts in this direction to implement natural pigments in every industry that uses pigments are needed urgently to arrest industrial emissions and to overcome environmental pollution, global warming, and climate change. The combination of green-energy-based industries and pigmented microbes could pave the way to reducing the industrial-based atmospheric and liquid chemical effluents. It is the need of the hour to understand the importance of the ecosystem rather than showing interest in color-appealing things (originated from industries) without knowing their (toxic emissions released from an attractive product that uses synthetic colorants) negative impacts on the environment and health. In addition, utilizing natural substrates over synthetic chemical substrates in any fermentation system may indirectly reduce the industrial emissions (by reducing synthetic chemical demand and emissions released from chemical manufacturing industries) into the atmosphere.

Light-harvesting primary pigments are known to capture CO_2 from the atmosphere. It is evident that many bacterial and fungal species found in agroecosystems [173] as well as aquatic microbes, especially marine microbes [174–176], are directly involved in carbon sequestration. However, little is known about the role of pigmented bacteria, fungi, and yeast in CO_2 sequestration, indicating the research gap to be studied. Nevertheless, pigments originating from microbes, especially bacteria (pigmented fungi and yeast are the least studied in this context), could indirectly help CO_2 capture by acting as potential growth promoters of plants [177,178] and biocontrol agents of phytopathogens [177–179] and insects [180]. Prodiginine obtained via mutasynthesis in *Pseudomonas putida* was reported to enhance the root growth of *Arabidopsis thaliana* at low concentrations [178]. *Serratia marcescens* isolated from cattle manure vermicompost [177] and halotolerant bacteria *Bacillus* and *Halobacillus* isolated from groundnut plants' rhizosphere [180] showed growth-promoting abilities [177,181] and inhibited phytopathogenic fungi [177]. The prodigiosin pigment of *S. marcescens* isolated from *Digitaria decumbens* grass compost [179] and the rhizosphere of *Bacopa monnieri* acted as a biocontrol agent to phytopathogens [182]. Cell-free culture filtrates of pink pigmented *Methylobacterium* strains when added with 1.09 to 9.89 $\mu g \cdot mL^{-1}$ of cytokinins showed a seed germination effect on wheat *Triticum aestivum* [183]. Liquid extracts from *Spirulina platensis* showed a seed germination effect on the groundnut *Arachis hypogaea* [184]. These studies indicate that microbial pigments could protect plants from phytopathogens, promote plant growth, and indirectly facilitate CO_2 capture by protecting plants from chloroplast damage and photosynthesis arrest.

Fungal species have also been shown to be involved in CO_2 sequestration, in particular, soil fungi dramatically benefit the environment and ecosystem in a positive way [185].

Numerous research studies have shown that arbuscular mycorrhizal fungi (AMF) play a role as climate change warriors. The mycorrhizal fungi have a symbiotic relationship with plants by colonizing the root cells, where they form a large hyphal network and exert major control on transporting carbon [186–188]. In addition, the symbiotic association of fungi with plants has fundamental effects on the plant physiology and growth, and especially helps to utilize phosphorus and nitrogen, thus aiding in stimulating plant growth. For example, hyphae of AMF produce a glycoprotein called glomalin, which protects hyphae against nutrient or water losses, glues together soil aggregates, and improves nutrient cycling as well as nutrient uptake in plants [189,190]. Similarly, AMF of the phylum Glomeromycota boost water and nutrient exchange in plant roots through their hyphae [191,192]. Many *Rhizobium* spp., colonize the plant root cells of some plants of the legume family, which helps in nitrogen fixation [193].

Ectomycorrhizal fungal (EMF) species of *Suillus*, *Piloderma*, and *Cortinarius* are predominant in boreal forests and are likely to play a crucial role in storing soil carbon in mycorrhizal forests [194,195]. Furthermore, species of *Suillus* and *Cortinarius* are involved in forest restoration and are linked to rapid turnover of microbial biomass and efficient nitrogen utilization in the forest plants [196]. In addition to these benefits, it was reported that several species of *Trichoderma* have been used as successful biocontrol agents owing to this potential action against phytopathogens. In a study by Lombardi et al., it was found that *Trichoderma* spp. stimulated strawberry plant growth, improved fruit yield, and improved the accumulation of anthocyanins and antioxidants in red ripened fruits [197]. *Piriformospora indica* also exhibited a multifunctional role in diverse plant species mainly by regulating plant metabolism and improving plant tolerance to various biotic and abiotic stresses [198]. Considering the role of fungal pigments in carbon sequestration and their influence on ecosystem function, little is known. However, it was demonstrated that the highly melanized fungus *Cenococcum geophilum* is drought-tolerant in water-stressed habitats. It is suggested that melanin is an important functional trait that allowed the hyphae to penetrate deeper into the soil to access water, and it is considered that melanin production helps with this function [199]. Hence, by closely work together with plants, fungal communities can potentially strengthen their defense mechanisms, improve resilience to plant diseases, enhance nutrient uptake through well-developed roots, store soil carbon, and so on.

Although several species of yeast have demonstrated plant-growth-promoting ability [200], the ability of pigmented yeast to promote plant growth has not been studied, whereas, similar to macroalgal culture beds [201], several investigations found that large-scale culture of microalgae in open systems, bioreactors [202–209], and integrated culture systems [210] play an important role in the mitigation of atmospheric CO_2. In this way, bacteria, fungi, and microalgae offer multifaceted applications to society and protect the environment by regulating CO_2 levels.

10. Current Applications of Microbial Pigments

The numerous applications of microbial pigments in food, textile, leather, cosmetic, and drug industries have been reviewed very often in the last five years by various authors [1,2,114,164,211–214]. Here, we detail the selected and recent applications of microbial pigments in various areas. Undecylprodigiosin, a prodigiosin pigment derivative, was reported to have dyeing, food colorant, and antimicrobial properties [162,215]. Particularly, undecylprodigiosin and other unidentified pigment molecules have been demonstrated to show a high affinity to staining transverse sections of *Tridax procumbens* [162], indicating the application of these pigments as natural stains in laboratory studies. Recently, the prodigiosin pigment extracted from *Serratia plymuthica* has been used to develop an antibacterial (against *S. aureus* and *P. aeruginosa*) food packaging system in combination with bacterial cellulose and a chitosan composite [216]. Similarly, the development of antimicrobial textiles for hospital-acquired infections has been demonstrated using prodigiosin extracted from *Serratia rubidaea* [217]. The flexirubin pigment extracted from *Chryseobac-*

terium artocarpi was used to make soaps [113]. Tyrian purple indigoid (originated from *Murex*) synthesized from *E. coli* has potential dye applications [218]. Indigoid pigments are reported to have chemosensory and semiconductor properties [219]. Phycocyanin extracted from *Arthrospira platensis* is used as a fluorescent probe in medical, food safety, and environmental research [71,220]. Microalgae is one of the major sources of nutraceuticals, pharmaceuticals, and biogases [84], especially having anticancer properties [27,221,222]. Thus, microalgae-based pigments have also been gaining more attraction in the industry compared to bacterial and fungal pigments.

11. Future Directions of Microbial Pigments

Pigmented microbes have been widely explored for multifaceted applications in various industries. However, the evolutionary importance of microbial pigments is least understood. Therefore, the origin of pigmented genes and pigment molecules from a wide range of microbes (bacteria, fungi, yeast, cyanobacteria, and microalgae) distributed in different environments such as marine, aerobic, terrestrial, and estuarine are needed to be explored intensively to understand their convergent and divergent evolutionary patterns in the tree of life. On the other hand, pigmented microbes are known to be abundant in the marine environment and have demonstrated potential biological properties. Nevertheless, marine pigmented microbes have largely remained unexplored. Furthermore, the use of various agro-wastes, poultry waste, and fish waste need to be utilized in submerged fermentation to test the stimulation efficiency of these substrates to yield high pigment production from microbes. Thus, further research on these less-studied research gaps is essential to explore the ecological, evolutionary, and societal benefits of microbial pigments.

12. Conclusions

Microbial pigments have proven to offer multifaceted applications to a wide range of industries, including biomedical, textile, leather, food, and drug industries. It is evident that synthetic pigments pose toxic effects on the environment and biota, including humans. Therefore, the production of pigments from potential microbes needs to be implemented intensively in submerged fermentation. The use of natural agro-industrial residues in submerged fermentation has proven to yield more pigments and reduced the production costs of pigments in various industries. Therefore, submerged fermentation is inferred as a convenient and effective method to understand the synergetic effect of substrates and culture conditions on pigment production from potential microbes. This strategy would undoubtedly fulfill the industrial needs and eliminate risks posed by synthetic pigments used in food and drugs.

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