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Bacterial Pigments As Biosynthetic Platforms: A Systematic Review Of Current Evidence

Delna N S[1*], Dr. Renu Mishra[2], Dr. Anil Prakash[3], Nabiya Sadaf[4], Vaishnavi Kumar[5], A Lavanya[6], Dr. Lalitha Soumya Johnson[7]

[1*]Department of Microbiology, Barkatullah University, Bhopal, India
[2]Department of Botany and Microbiology, Sri Sathya Sai College for Women, Bhopal, India
[3] Centre for Sustainable Agriculture and Environment; A R&D Centre of Professor HS Srivastava Foundation for Science and Society, Lucknow, India
[4]Chandigarh University, Mohali, India
[5]Sapthagiri Institute of Medical Science and Research Centre, Bangalore, India
[6]Universal Group of Institution, Bengaluru Karnataka, India
[7]Department of Biotechnology & Microbiology, Dr. Janaki Ammal campus, Kannur University, Kerala, India
[*]**Corresponding Author:** Delna N S
[*]Department of Microbiology, Barkatullah University, Bhopal, India

Abstract

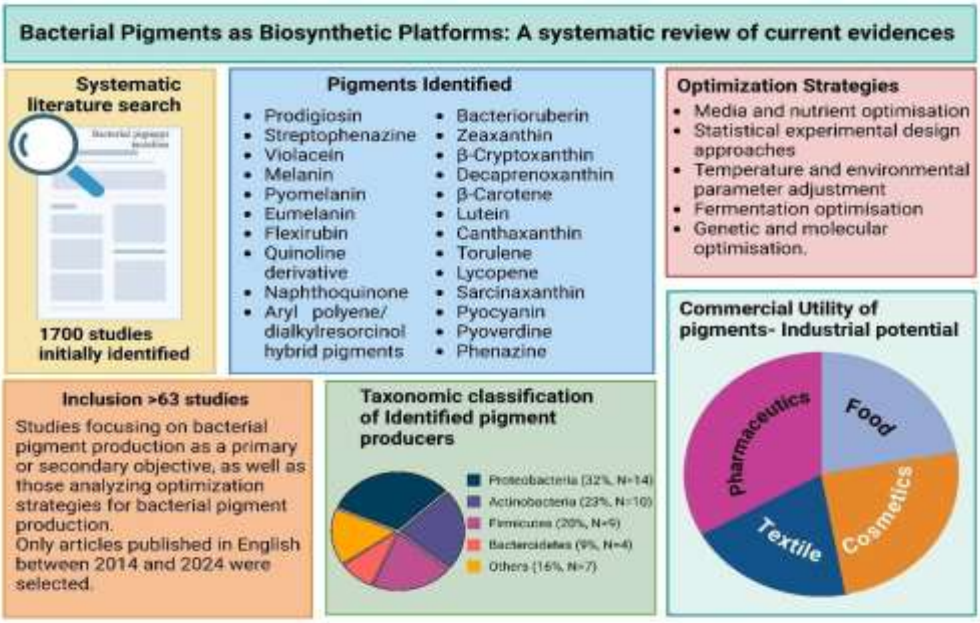
Aim & Objectives: *Bacterial pigments, a class of bioactive secondary metabolites, are gaining global interest as sustainable alternatives to synthetic dyes due to their antioxidant, antimicrobial, and UV-protective properties. This systematic review aimed to identify and classify pigment-producing bacterial species, evaluate optimisation strategies for enhancing pigment production, and assess practical industrial applications and commercial scalability of bacterial pigments.*

Methods: *This review was conducted in accordance with the PRISMA 2020 guidelines to ensure methodological transparency and standardized evidence synthesis. A comprehensive database search was performed to retrieve studies published in English between 2014 and 2024. Eligible studies were those that included experimental work identifying bacterial pigments and incorporated optimization techniques for pigment production. Studies focusing on nonbacterial pigment sources, review articles, and those lacking pigment identification or optimization analysis were excluded. Data extraction and quality assessment were carried out independently by multiple reviewers, ensuring that only studies with sound methodology were included in the final qualitative synthesis.*

Results: *Out of 1,700 initially screened articles, 63 met the inclusion criteria. A total of 84 pigment-producing bacterial species and 24 unique pigments were identified, categorized into eight pigment classes: carotenoids, phenazines, prodigiosins, violaceins, melanins, flexirubintype pigments, quinones/naphthoquinones, and polyketides. Optimization strategies included media and nutrient formulation, fermentation condition tuning, statistical design approaches, and genetic engineering.*

Conclusion: *Bacterial pigments are a promising avenue for sustainable pigment production with broad industrial potential. While substantial progress has been made in pigment optimization and application, further interdisciplinary research is needed to overcome barriers to large-scale manufacturing and regulatory approval.*

Keywords: *Bacterial pigments, Secondary metabolites, natural colourants, systematic review.*



Studies focusing on bacterial pigment production as a primary or secondary objective, as well as those analyzing optimization strategies for bacterial pigment production.
Only articles published in English between 2014 and 2024 were selected.

INTRODUCTION

The number of studies being conducted on bacterial pigments, their isolation, and purification is increasing day by day (N S et al., 2024). What are bacterial pigments, and why do they garner significant attention nowadays? Over the last decade, researchers worldwide have been actively isolating and identifying new bacterial strains and their pigments. This trend is largely driven by the increasing demand for bio-based pigments in the pharmaceuticals, biotechnology, food, cosmetics, and textiles industries. According to a market analysis from over 30 countries, the bio-based pigment market is projected to reach $48.58 billion by 2034, with bacterial pigments being of particular interest due to their ease of production and the relatively quick turnaround from bacterial cultures (Bio-based pigment and dye market outlook).

Bacterial secondary metabolites are bioactive compounds produced by microorganisms that are not directly involved in growth, development, or reproduction (Srinivasan et al., 2021). Unlike primary metabolites such as amino acids, nucleotides, and carbohydrates, which are essential for cellular functions, secondary metabolites are synthesized under specific environmental conditions and often serve ecological roles, such as antimicrobial defence, competition, and signalling (William et al., 1989; Ruiz et al., 2010).

These pigments provide protection against UV radiation, oxidative stress, and predation, and some exhibit antimicrobial and antioxidant properties (Fariq et al., 2019). Bacterial pigments can be categorized into various chemical classes, including carotenoids, melanins, phenazines, prodiginines, violaceins, and flexirubin-type pigments. The synthesis and production of these pigments are significantly influenced by several factors, including bacterial strain, nutrient availability, pH, temperature, oxygenation, and medium composition (van et al.,1946; Malik et al.,2012).

Given the evidence that bacterial pigments of commercial importance can be produced and that their yields can be enhanced through proper optimization strategies, our systematic review aims to compile and analyze recent advancements in bacterial pigment research. We will focus on studies that examine bacterial pigment production capabilities and enumerate their properties. This study will be a valuable compilation of recent developments in bacterial pigment research, serving as a summary for ongoing efforts and accelerating future research initiatives.

MATERIALS AND METHODS

This systematic review was conducted according to the published protocol available in the Open Science Framework (OSF) registries (Link: https://doi.org/10.17605/OSF.IO/W7C3R) and reported following the PRISMA 2020 guidelines to ensure transparency and reproducibility.

INCLUSION CRITERIA

Studies focusing on bacterial pigment production as a primary or secondary objective, as well as those analysing optimisation strategies for bacterial pigment production (e.g., genetic, metabolic, environmental), were included. We considered, but were not limited to, experimental studies, randomized controlled trials, and pilot studies on pigment yield improvement. Only articles published in English between 2014 and 2024 were selected.

EXCLUSION CRITERIA

Studies focusing on pigments from non-bacterial sources (e.g., fungi, plants), non-experimental studies, editorials, and opinion pieces, as well as studies without clear discussions on optimization strategies or applications, or those that did not identify the pigment-producing bacteria, were also excluded from the review.

STUDY SELECTION AND QUALITY ASSESSMENT

The articles were reviewed independently by two authors, and any disagreements were resolved through consensus with a third author. The reasons for excluding studies were documented. Data extraction was performed independently by three authors using data extraction forms. Since no specific tool was available for quality assessment, each study was individually reviewed to ensure that a sound methodology was employed. We verified that all studies accurately analyzed pigment-producing bacteria, properly extracted the pigments from pure cultures, identified them using valid techniques, and implemented optimization strategies to enhance pigment production capabilities.

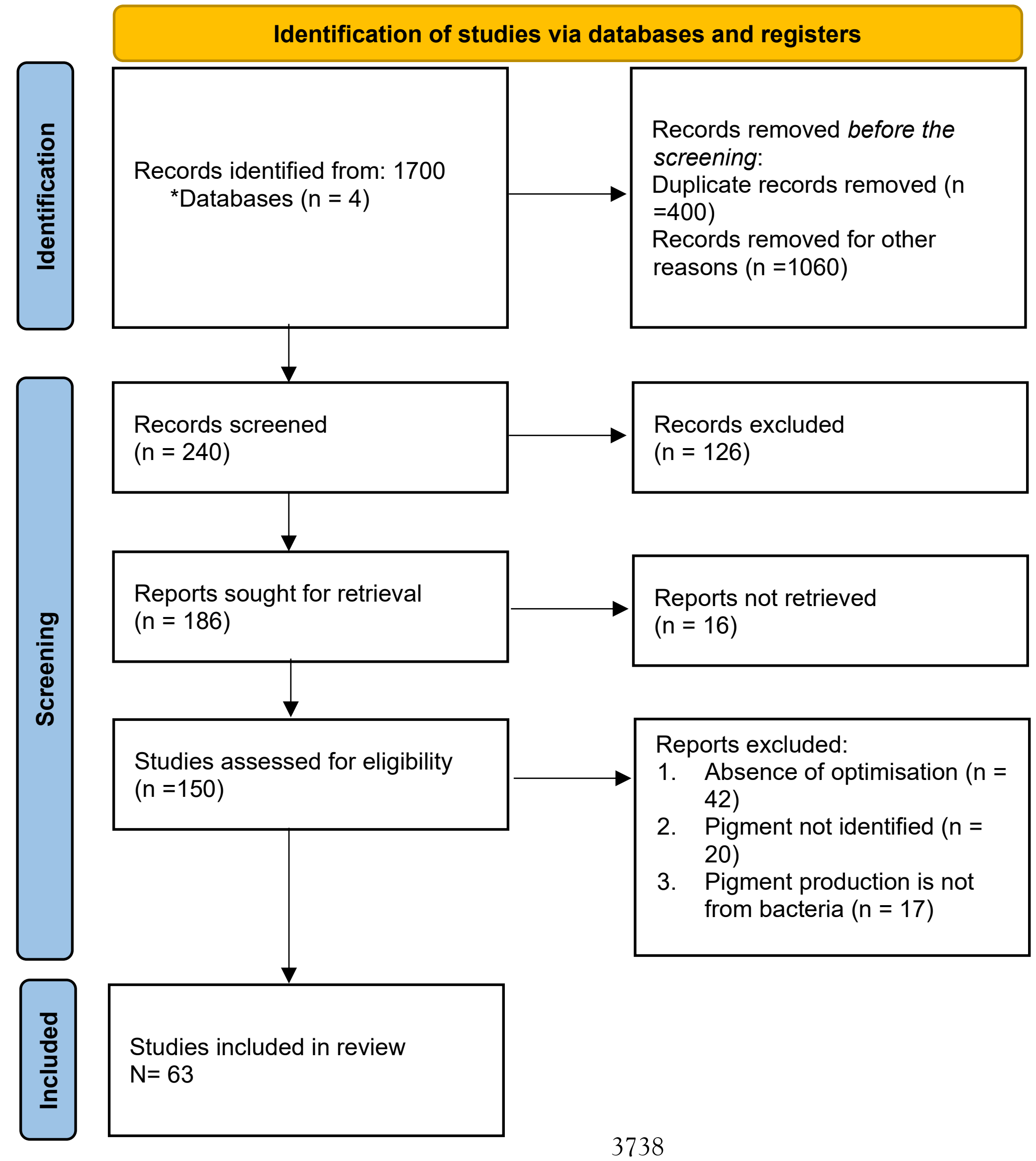


Table 1: Full data extraction table of reviewed studies.

Reference	Bacteria isolated from	Identified bacterial strains	Optimisation Strategies for Pigment Production	Pigment produced
Amorim et al., 2022	Purchased from Leibniz Institute DSMZ-German Collection of Microorganisms and Cell Cultures (DSMZ, Braunschweig, Germany)	1. **Serratia plymuthica** 2. **Chryseobacterium shigense**	Prodigiosin was optimized with a fermentation process using peptone, glycerol phosphate (PGP) medium, and Flexirubin-type optimized by adjusting aeration and agitation in nutrient medium.	1. Prodigiosin 2. Flexirubin
Shahin et al., 2022	Soil	**Micrococcus lylae**	Central composite statistical design to maximize the biomass production, pigment concentration, and antimicrobial activity of the pigment.	Echinenone (β-carotene pigment)
El-Batal et al., 2017	Soil	**Streptomyces cyaneus**	Plackett–Burman design (P-BD), while further statistical optimization was applied using Central Composite Design (CCD) for maximizing yield.	Melanin
Silva et al., 2019	1. Shells found on bird nests (Arthrobacter agilis 50cyt) 2. Icefrost biofilm (Arthrobacter psychrochitiniphilus 366) 3. Sea sponge (Zobellia laminarie 465)	1. **Arthrobacter agilis 50cyt** 2. **Arthrobacter psychrochitiniphilus 366** 3. **Zobellia laminarie 465**	Cultivation in nutrient broth at 15°C, extraction of carotenoids, photostability, and antioxidant tests.	Carotenoids: 1. Bacterioruberin, 2. Decaprenoxanthin 3. Zeaxanthin, 3. β-Cryptoxanthin, 3. Phytoene
Nanaware et al., 2024	Soil	1. **Streptomyces** 2. **Pseudomonas** 3. **Bacillus** 4. **Serratia** 5. **Chromobacterium**	~	1. Carotenoids, 2. phenazines, 3. melanin, 4. Flavonoids
Korumilli et al., 2014	Marine water, garden soil, and purchased strains.	1. **Pseudomonas guinea** 2. **Bacillus safensis** 3. **Bacillus clausii**	Use of vegetable waste, fruit waste extract (FWE), Taguchi method, response surface techniques	1. Melanin 2. β-Carotenoid 3. Torularhodin 4. Astaxanthin
HM et al., 2019	Liquid pineapple waste (LPW)	**Chromobacterium violaceum**	Response Surface Methodology (RSM)	Violacein
Noby et al., 2023	Air and soil samples	**Arthrobacter agilis NP20**	Box-Behnken Design (BBD) optimization on whey-based medium (96% sweet whey with $MgSO_4$ and yeast extract)	1. Bacterioruberin 2. bis-anhydrobacterioruberin, 3. mono-anhydrobacterioruberin, 4. glycosylated bacterioruberin
Ramesh et al., 2020	Seawater, sediment, marine plants, invertebrates, and vertebrates	**1. Zooshikella sp. (S2.1)** **2. Streptomyces sp. (BSE6.1)**	Cultivation in different media (Marine agar, Nutrient agar, etc.) and incubation at 32°C and room temperature for 7–10 days Temperature and pH optimization (e.g., dark red pigment at pH 1, yellow at pH 12).	1. Prodigiosin 2. Streptophenazine

A Salehi Bakhtiyari et al., 2020	Soil samples	1. **Staphylococcus aureus (S4O)** 2. **Micrococcus luteus (S11Y)** 3. **Micrococcus roseus (S14P)** 4. **Pseudomonas aeruginosa (S17G)**	Response Surface Methodology	1. Carotenoids (S4O, S11Y, S14P), 2. Pyocyanin (S17G)
Raman et al., 2023	Freshwater	**Flavobacterium sp. JSWR-1**	Optimization of light-irradiation, pH, temperature, and carbon/nitrogen sources; fed-batch fermentation	Zeaxanthin
Kumar et al., 2024	Marine sample	**Arthrobacter sp.**	One-factor-at-a-time approach for production optimization	Carotenoid-related pigment
Venil et al., 2021	Enteric gut of sulfur butterfly	**Serratia marcescens SB08**	Optimization of pH, temperature, reaction time, color intensity, and fastness properties for textile dyeing	Prodigiosin
Mandal et al., 2023	Arctic soil	**Kocuria indica (RSAP2)**	Culture media optimization for NaCl, pH, incubation time, and agitation.	Quinoline derivative
Mukhia et al., 2024	Glacial moraine	**Janthinobacterium sp. ERMR3:09**	1.0% glucose, 0.08% peptone, pH 7, 20°C; upscaled to 8 L volume; 48 h production	Prodigiosin
Jinendiran et al., 2019	Soil samples	**Exiguobacterium acetylicum S01**	Glucose (1.4 g/L), peptone (26.5 g/L), pH 8.5, temperature 30°C, optimized in 5-L bioreactor	β-Carotene
Marey et al., 2024	Clinical isolates	**Pseudomonas aeruginosa**	Cultivation on cetrimide agar for pigment production	Pyocyanin
Sulaiman et al., 2016	Macroalgae, corals, animal resources, sand, seawater, fish net	**Pseudoalteromonas rubra**	Shake flask culture optimization	Prodigiosin (red pigment)
Ghosh et al., 2020	Environmental samples (soil, air, mangroves).	**Serratia nematodiphila**	Nutrient broth with 0.2% mannitol and 0.2% inorganic phosphate, 1% NaCl, pH 8, incubation at 25°C for 48 h	Prodigiosin
Alem et al., 2020	Antarctic bacterial isolate	**Janthinobacterium svalbardensis**	Tryptic Soy Broth medium with 3.6 g/L glucose at 20 °C; scaled up in a 5 L bioreactor (yield doubled)	Violacein
Marín et al., 2022	Hot spring sediments	**Bacillus haynesii CamB6**	Temperature (50-60 °C), pH (5.0-7.0), nitrogen/carbon sources (1-5 g·L-1), salinity stress (19.45 g·L-1 NaCl), fed-batch cultivation	Pyomelanin
Amorim et al., 2022	Kombucha Culture	1. **Serratia plymuthica** 2. **Chromobacterium violaceum** 3. **Chryseobacterium shigense**	Full Factorial Design (Optimization of temperature, duration, and pigment concentration)	1. Prodigiosin 2. Violacein 3. Flexirubin-type pigment
Pallath et al., 2024	Facial acne	**Serratia marcescens**	pH 4, 72 hours incubation at 37 ± 2°C; yield: 15.56 g/L	Prodigiosin
Mendes et al, 2021	Soil (0–20 cm layer) in the Caatinga biome.	**Kocuria palustris strains FT-5.12 and FT-7 22**	Temperature (30°C and 40°C), luminosity (light and dark), agitation (180 rpm and 250 rpm), and aeration	Sarcinaxanthin

			(presence or absence of plastic spiral).	
Zeleke et al ., 2024	Soil and environmental sources	1. **Kocuria rosea** 2. **Micrococcus luteus** 3. **Exiguobacterium auranticum**	Agro-waste extracts as substrates (e.g., orange waste); temperature (28–45°C), pH (6–10), agitation (60–120 rpm), salt concentration (1–5%), 1% glucose, 0.1% yeast extract.	Carotenoid pigment
Benjamin et al., 2016	Environmental samples	**Micrococcus luteus** BAA2	Optimized conditions: 28°C for growth (pH 7, 24 h), 36 h for maximum pigment production (pH 7)	carotenoid pigment
Suryawanshi et al., 2015	Soil and Water	1. **Serratia marcescens** 2. **Chromobacterium violaceum**	Optimized growth conditions: temperature, pH, medium composition, pigment concentration at 4% for SPF enhancement	1. Prodigiosin 2. Violacein
Rhenals et al., 2024	Laboratory cultures	**Gordonia hongkongensis strain EUFUS-Z928**	Optimized inoculum concentration, temperature, and agitation speed using Plackett-Burman design and RSM	Carotenoid pigments
Seo et al., 2024	~	**Pseudomonas aeruginosa**	Sequential treatment with a surfactant-based dressing; Imaging and staining methods for biofilm evaluation	Chromophores
Silva et al., 2016	Laboratory cultures	**Gordonia alkanivorans**	Optimized for glucose-sulfate-light culture conditions	Carotenoids - 1. Lutein 2. Canthaxanthin 3. Astaxanthin
Elbargisy et al., 2021	Urinary tract infection isolates	**Pseudomonas aeruginosa**	Optimized conditions: King's A fluid medium at pH 7, 37 °C, shaking at 200 rpm for 3-4 days	Pyocyanin
Hegazy et al., 2024	Laboratory culture	**Micrococcus luteus** (ATCC 9341)	BOX-Behnken design to optimize whey concentration, inoculum size, pH, temperature, and agitation speed. Achieved 2.19 g/L yield, productivity 0.045 g/L^{-1} h^{-1}, yield 0.644 g/g.	Carotenoids
Abdelaziz et al., 2022	Laboratory culture	**Pseudomonas aeruginosa**	pH-adjusted peptone water with 3% cetrimide, shaking conditions at 37°C for 3 days, yielding 53 µg/ml of pyocyanin. Lyophilization enhanced shelf-life to 1 year.	Pyocyanin
Kothari et al., 2022	Respiratory tract, urinary tract, vascular system, and CNS	**Pseudomonas aeruginosa**	King's A medium agar	1. Pyoverdine: Yellow pigment 2. Pyocyanin: Green pigment
Lazic et al.,2022	Commercially available strain	**Serratia marcescens**	Nutrient media optimization, pH 7, temperature 30°C, agitation rate 200 rpm	Prodigiosin
Venil et al., 2014	Orchard in Universiti Teknologi Malaysia	**Chryseobacterium sp. UTM-3T**	Submerged fermentation, cultivation at 30°C, 200 rpm, extraction using acetone and ultrasonication	Flexirubin pigment

Sricharoen et al.,2022	Salty fermented foods	1. **Halobacillus yeomjeoni** 2. **Salinicoccus sp. (82-1)** 3. **Bacillus infantis (63-11)** 4. **Bacillus amyloliquefaciens (60-5)** 5. **Staphylococcus carnosus (48-10)**	The strains were cultivated in nutrient broth (NB) containing 3% sodium chloride (NaCl) under orbital shaking (150 rpm) at room temperature for 4 days.	Carotenoid derivatives: 1. Lycopene 2. Lutein 3. β-carotene
Neelam et al ., 2019	Sambhar Lake, Rajasthan	**Piscibacillus sp. C12A1**	Optimal conditions: 10–15% NaCl, pH 8, temperature 37°C	Carotenoids
da Silva et al., 2022	semi-arid soil	**Serratia marcescens**	Optimized production using low-cost corn bran substrate; growth yield 7.24 g/L; pigment yield 1.68 g/L	Prodigiosin (red pigment)
Ferraz et al., 2021	Goat cheese rind	**Pseudomonas putida** ESACB 191	Produced in synthetic Müeller-Hinton Broth; productivity 1.57 mg/L/h	Eumelanin (brown pigment)
Mohammad et al., 2024	Urine and urinary catheter	**Serratia marcescens**	LB medium supplemented with sesame powder yielded the highest pigment production (179.398 and 107.280 units/cell for S1 and S2)	Prodigiosin (red pigment)
Vishnu et al., 2016	Soil and water	1. **Chromobacterium violaceum CV4** **2. C. vaccinii CV5**	Culture media, incubation time, and temperature optimization.	Violacein (violet pigment)
Sahoo et al., 2019	Soil from Karwar mangrove regions, Karnataka	1. **Pseudomonas aeruginosa (KA16SPiv)** 2. **Salinicoccus roseus (KA16SK2HS)**	Optimal conditions: pH 8, 37°C; pigments extractable in chloroform and methanol	1. Phenazine skeleton (Fluorescent green) 2. Prodigiosin skeleton (pink)
Efimova et al., 2023	Laboratory study	**Janthinobacterium lividum**	Submerged cultivation at 25°C; stimulated violacein production under 0.003% H_2O_2 conditions	Violacein
Mahatmanto et al., 2022	Rhizosphere of Mimosa pudica	**Chryseobacterium sp.**	Adaptation through 30 passages with feathers as the sole carbon and nitrogen source.	1. Flexirubin (yellow pigment)
El-Fouly et al., 2015	Soil, water, and clinical specimens	**Pseudomonas aeruginosa** R1 (rice soil) and U3 (UTI specimen)	Designed a cost-effective medium (cotton seed meal + peptone), improved production by 30.1% (R1) and 17.2% (U3) while reducing costs by 56.7%	Pyocyanin
Patkar et al., 2021	Mangrove rhizosphere habitat- Soil bacteria	1. **Bacillus infantis (MZ)** 2. **Halomonas sp.** (Orange), 3. **Bacillus sp.** (Yellow)	~	Carotenoid pigment
Afra et al.,2017	Marine environment	**Arthrobacter sp.**	One-factor-at-a-time approach to optimise pigment production	Carotenoid-red pigment
Moura et al., 2014	Laboratory studies	1. **Pseudomonas aeruginosa** 2. **Mycobacterium tuberculosis**	~	1. Phenazines 2. Naphthoquinone (phthiocol)
Schöner et al. 2016	Cultured in LB medium	**Variovorax paradoxus B4**	Arcuflavin A yield: 93.6 nmol/g dry weight	Aryl polyene/dialkylresorcinol hybrid pigments (arcuflavins A and B)

Mukhia et al. 2023	Sikkim Himalaya	**Janthinobacterium sp. ERMR3:09**	Optimal production under cold stress	Prodigiosin (red pigment)
Kanelli et al. 2018	Laboratory study	**Janthinobacterium lividum**	˜	Violacein
Elkenawy et al. 2017	Biodiesel-derived crude	**Serratia marcescens MN5**	Maximum production: 870 unit/cell; doubled under gamma radiation	Prodigiosin
El-Batal et al. 2017	Laboratory study	**Streptomyces cyaneus**	Maximum yield: 11.113 mg/mL (with gamma irradiation)	Melanin
Lin et al. 2019	Soil in Fuzhou	**Serratia marcescens FZSF02**	Maximum production: 15,420.9 mg/L; 62.3% in pigment pellet form	Prodigiosin
Aruldass et al. 2015	Liquid pineapple waste	**Chromobacterium violaceum UTM5**	Maximum production: 16,256 ± 440 mg/L in optimized medium	1. Violacein, 2. Deoxyviolacein
Mukhia et al. 2023	Agro-industrial waste (onion peels, potato skin, mung bean husk, pea pods)	**Janthinobacterium sp, ERMR3:09**	Over 100 µg carotenoids per g dry biomass under optimized conditions	Prodigiosin (red pigment)
Bolognese et al., 2019	Recombinant system	**Escherichia coli JM109**	- Growth in mineral medium with 10 mM glucose+ Addition of casamino acids (0.2% w/v) + Tyrosine 1 mM added after 30 min of exposure to 1% arabinose+ 6-day biotransformation	Pyomelanin
Silva et al ., 2019	Soil	**Streptomyces fildesensis**	Optimization of M1 medium containing peptone, yeast extract, starch, and pH adjustment to 7.0. Incubation at 15°C with constant agitation for 6 days. Spectrophotometric and Fourier Transform Infrared Spectroscopy (FTIR) for pigment characterization.	Melanin-like pigment
Wang et al ., 2020	Laboratory-engineered	**Vibrio natriegens**	Expression of the tyrosinase gene under inducible promoters, optimized with IPTG, L-tyrosine supplementation, salt concentration, and pH adjustments	Melanin
Vila et al., 2019	Various ecological samples	1. **Arthrobacter** **2. Flavobacterium** **3. Cryobacterium** **4. Salinibacterium** **5. Planococcus**	Use of sub-Antarctic bacterial strains; focus on psychrophilic growth conditions	Carotenoids: 1. Zeaxanthin 2. β-carotene
Xi-Ran et al, 2015	Laboratory-engineered E. coli	**Escherichia coli (LYCOP strain)**	TIGR (tunable intergenic regions) and protein fusion methods for balanced crtY and crtZ gene expression.	Zeaxanthin
Skogman et al., 2016	Laboratory studies	1. **Chromobacterium violaceum ATCC 31532**	Optimization of growth media (TSB, LB with additives), addition of 0.5 µM C6-HSL autoinducer, and ethanol for violacein extraction	Violacein

RESULTS AND DISCUSSION

The systematic literature search initially retrieved 1,700 studies. From these, we selected 63 studies that followed proper methodology to isolate and identify bacteria and performed optimisation strategies to enhance pigment production. Forty-two studies were excluded due to the absence of data on optimization for pigment production or for not attempting optimization. Twenty studies were excluded as they did not perform any analysis to identify the pigments, and 17 studies were excluded because the pigment originated from non-bacterial sources (see Table 1 for full data extraction).

We identified 84 pigment-producing bacterial species and 24 bacterial pigments with potential applications in various industries, including pharmaceuticals, biotechnology, textiles, cosmetics, and food. The identified bacterial pigments can be classified into eight categories (see Table 1), and taxonomic classification of identified species includes *Actinobacteria*, Proteobacteria, Firmicutes, Bacteroidetes, and other bacterial groups like *Exiguobacterium acetylicum S01*, *Exiguobacterium auranticum*, *Cryobacterium*, *Salinibacterium*, *Planococcus*, and *Piscibacillus sp. C12A1*, *Mycobacterium tuberculosis* (See Figure 2).

Classification of identified pigments	
Carotenoids	• Bacterioruberin • Zeaxanthin • β-Cryptoxanthin • Decaprenoxanthin • β-Carotene • Lutein • Canthaxanthin • Torulene • Lycopene • Sarcinaxanthin
Phenazines	• Pyocyanin • Pyoverdine • Phenazine
Prodigiosin Group	• Prodigiosin • Streptophenazine
Violacein Group	• Violacein
Melanin Group	• Melanin • Pyomelanin • Eumelanin
Flexirubin-Type Pigments	• Flexirubin
Quinones and Naphthoquinones	• Quinoline derivative • Naphthoquinone
Polyketides	• Aryl polyene/dialkylresorcinol hybrid pigments

Table 1: Shows the classification of 24 bacterial pigments identified in the review.

Gram-positive pigment producers	**Gram-negative pigment bacteria**
Arthrobacter agilis	*Chromobacterium violaceum*
Arthrobacter psychrochitiniphilus	*Chromobacterium vaccinii*
Bacillus safensis	*Chryseobacterium shigense*
Bacillus clausii	*Escherichia coli JM109*
Bacillus amyloliquefaciens	*Escherichia coli (LYCOP strain)*
Bacillus infantis	*Exiguobacterium acetylicum*
Bacillus haynesii	*Janthinobacterium lividum*

Gordonia hongkongensis	*Janthinobacterium svalbardensis*
Gordonia alkanivorans	*Pseudomonas aeruginosa*
Kocuria indica	*Pseudomonas putida*
Kocuria palustris	*Pseudomonas guinea*
Kocuria rosea	*Pseudoalteromonas rubra*
Micrococcus luteus	*Rhodotorula mucilaginosa*
Micrococcus roseus	*Serratia marcescens*
Mycobacterium tuberculosis	*Serratia nematodiphila*
Staphylococcus aureus	*Serratia plymuthica*
Staphylococcus carnosus	*Variovorax paradoxus*
Streptomyces cyaneus	*Vibrio natriegens*
Streptomyces fildesensis	*Zobellia laminarie*

Table 2: Classification of Pigment-Producing Bacteria Based on Gram-Staining Characteristics

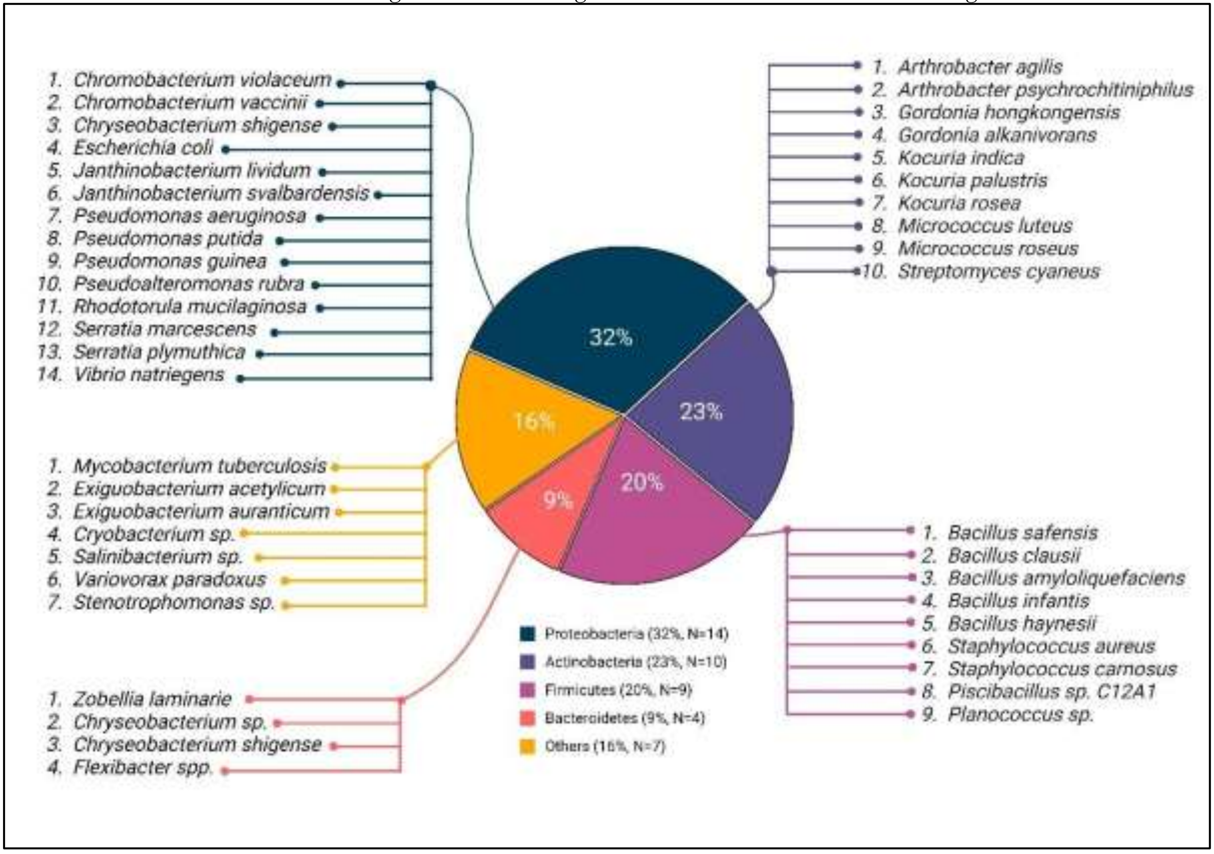


Figure 2: Taxonomic Classification of Pigment-Producing Bacteria Identified in the Systematic Review

OPTIMISATION STRATEGIES FOR ENHANCED PIGMENT PRODUCTION

The studies identified in the systematic review employed various optimisation strategies to enhance bacterial pigment production. The optimisation techniques employed in studies can be classified into: (1) media and nutrient optimisation, (2) statistical experimental design approaches, (3) temperature and environmental parameter adjustment, (4) fermentation optimisation, and (5) genetic and molecular optimisation.

1. Media and nutrient optimisation

Researchers focused on modifying carbon, nitrogen, and mineral sources to enhance pigment biosynthesis. Media such as peptone glycerol phosphate medium, whey-based medium with $MgSO_4$ and yeast extract, Cetrimide agar, King's medium, Potato dextrose agar, Nutrient broth with NaCl and phosphate, Luria-Bertani medium supplemented with sesame powder, and Mueller-Hinton broth are found to help in getting higher pigment concentrations (Yolmeh et al., 2016; Mukhia et al., 2024; Marey et al., 2024; Suryawanshi et al., 2015; Rhenals et al., 2024; Elbargisy et al., 2021).

The optimal culture condition for enhanced pigment production varied between each bacterial strain identified. But in general, the majority of the studies reported that maximum pigment was achieved when the culture pH was 7 to 8.5 and incubation temperature was variable from 25°C to 40°C; moreover, prolonged incubation time also seems to yield enhanced pigment production (Mendes et al., 2021; Adhikari et al., 2021; Pallath et al., 2024; Marin-Sanhueza et al., 2022; Gosh et al., 2020; Mukhia et al., 2024).

Enhancing culture media with additional quantities of salts, sugars, nitrogen sources, and other organic and inorganic compounds has shown satisfactory results in boosting pigment production. For instance, in a study focused on extracting prodigiosin from *Serratia nematodiphila*, researchers enriched the nutrient broth with mannitol, inorganic phosphate, and NaCl. With proper optimization of temperature and pH, pigment production became scalable (Gosh et al., 2020). Furthermore, incorporating additional carbon and nitrogen sources such as dextrose, malt extract, NaNO3, asparagine, glycerol, and starch into culture media significantly increased pigment yields compared to standard media (Jena et al., 2015; Mukhia et al., 2023).

NaCl concentration of 10-15% is reported to be an ideal range for optimum bacterial growth and pigment production. Salinity is also a stress as it induces specific metabolic pathways to increase pigment production (Marin-Sanhueza et al., 2022; Neelam et al., 2019).

2. Statistical experimental design approaches

Since the pigment production depends on multiple variables, several studies implemented statistical modelling and experimental design approaches to identify optimal culture conditions systematically. Some studies used "Response Surface Methodology (RSM)" to optimize multiple interacting factors such as temperature, pH, and nutrient concentration. Studies employing RSM reported significant improvements in pigment yield due to the precise tuning of these variables (Salehi et al., 2020; Yatim et al., 2017). Box-Behnken Design (BBD) is another approach employed in studies for optimising pigment production (Noby et al., 2023; Lin et al., 2019). It is also a type of RSM used for optimizing processes by exploring the effects of multiple factors on a response variable by using a three-level experimental design (Lin et al., 2019).

Plackett–Burman Design (PBD) & Central Composite Design (CCD) methods were also used in some studies to determine the most influential factors affecting pigment biosynthesis and optimize experimental conditions with minimal resource expenditure (Noby et al., 2023; ElBatal et al., 2017; Shahin et al., 2022). CCD is also an RSM; on the other hand, PBD is a fractional factorial design used for screening experiments to identify significant factors.

3. Temperature and environmental parameter adjustment

Apart from media composition, studies also optimized physical and environmental parameters, including temperature, pH, light exposure, and salinity levels, to enhance pigment production (Njoku et al., 2024; Keekan et al., 2020). Among these physical parameters, the effect of incubation temperature was extensively studied. The studies show that mesophilic bacteria (*Serratia marcescens, Chromobacterium violaceum, Pseudomonas aeruginosa, Streptomyces cyaneus, Bacillus amyloliquefaciens, Micrococcus luteus)* produced maximum pigments at 30– 37°C, while psychrophilic strains (*Janthinobacterium lividum, Janthinobacterium svalbardensis, Zobellia laminarie, Arthrobacter psychrochitiniphilus*) require lower temperatures (~15°C) for optimal yield (da Silva et al., 2022; Ferraz et al., 2021; Efimova et al., 2023; Caliot et al., 2024; Aruldass et al., 2015; Mukhia et al., 2023).

Different species exhibited pH-dependent pigment production, most mesophilic bacteria preferred a neutral to slightly alkaline pH of 6.5 to 8.5, and many psychrophilic species produced maximum pigment yields at slightly acidic to neutral pH (5.5–7.5) (Neelam et al., 2019; Sahoo et al., 2019; Lee et al., 2014; Baltrus et al., 2024; Kanelli et al., 2018; Elkenawy et al., 2017; Sharma et al., 2020; Suwannarach et al., 2019; Zhao et al., 2019).

Alongside these enhancements, constant agitation, aeration, and exposure to light also contributed to higher pigment yields. Study by Elkenawy et al. (2017) on *Serratia marcescens* reports that exposure to gamma radiation enhances prodigiosin pigment production in this strain (Elkenawy et al., 2017; Elbargisy., 2021; Rhenals-Montoya et al., 2024).

4. FERMENTATION OPTIMISATION

Studies used fermentation techniques such as submerged fermentation, fed-batch fermentation, and solid-state fermentation to enhance pigment yield.

Submerged Fermentation (SmF): Performed at 30°C with 200 rpm agitation, this method ensured adequate oxygenation and nutrient availability, leading to increased bacterial growth and pigment production. SmF is widely used in industrial-scale production due to its ability to provide uniform aeration and efficient nutrient distribution (Venil et al., 2014; Efimova et al., 2023; Amorim et al., 2022).

Fed-Batch Fermentation: In this approach, nutrients were added incrementally, which resulted in sustained bacterial metabolism and prolonged pigment synthesis compared to batch fermentation. This approach will avoid nutrient depletion and toxic metabolite accumulation (Kanelli et al., 2018; Shahin et al., 2022).

Shake Flask Culture Optimization: Studies indicated that adjusting aeration and agitation rates in flask cultures significantly enhanced pigment production, especially in initial screening and laboratory-scale experiments. This simple and cost-effective method can be used in early-stage research before scaling up to bioreactors (Silva et al., 2019; Sahoo et al., 2019).

Solid-state fermentation (SSF): Even though it's not a widely used approach, SSF can be used as a cost-effective strategy to produce stable and high-yield bacterial pigments. Studies have adopted SSF in the bioconversion of waste materials into valuable pigments, which reduced production costs and scalability (Noby et al., 2023; Pallath et al., 2024).

Once the bacterial pigments are produced, efficient extraction and purification methods are necessary for commercial application. Strategies employed by studies for extraction and purification include: sequential surfactant-based treatment, chloroform and methanol-based extraction, and chromatographic purification techniques (Silva et al., 2019; Pallath et al., 2024).

5. GENETIC AND MOLECULAR OPTIMISATION.

Apart from the traditional approach for the optimisation of bacterial pigments, genetic and metabolic modifications have the potential to enhance the biosynthetic potential of bacterial pigments for commercial production.

Studies identified in our systematic review employed genetic modification, adaptive evolution techniques, and molecular engineering to increase bacterial pigment production. One of the most precise and effective methods adopted was the Tunable Intergenic Regions (TIGR) approach. This technique allows fine-tuned control of gene expression levels by modifying the intergenic DNA sequences between biosynthetic genes (Rhenals et al., 2024). Kanelli et al. (2018 implemented TIGR-based engineering in *Pseudomonas aeruginosa*, allowing for the balanced expression of crtY and crtZ genes, which are responsible for carotenoid biosynthesis. Another study by Rhenals et al., 2024 used protein fusion technology to improve the efficiency of violacein pathway enzymes, which resulted in a 2.3-fold increase in pigment production.

Bacterial pigments like melanin, prodigiosin, and carotenoids are regulated by complex biosynthetic pathways, and by using inducible gene expression systems, such as IPTG (Isopropyl β-D-1-thiogalactopyranoside), pigment production can be enhanced. Abdelaziz et al. (2022) successfully expressed tyrosinase genes under IPTG induction, resulting in a 1.7-fold increase in melanin production in genetically engineered *Escherichia coli,* and Hegazy et al. (2024) optimized violacein biosynthesis by upregulating key pathway enzymes using a recombinant expression system. This selective induction of pigment-related genes can enhance the host bacterial systems without requiring complex culture adjustments.

Adaptive evolution and mutation-based optimization are other approaches to genetically modify bacterial pigment producers. El-Batal et al., 2017 subjected *Serratia marcescens* to gamma radiation-induced adaptation, leading to a 67% increase in prodigiosin production.

Bolognese et al., 2019 found that exposing *Chromobacterium violaceum* to UV-induced random mutagenesis generated hyper-producing strains that retained stable pigment production across multiple generations.

Some studies explored the cold stress adaptation for psychrophilic pigment enhancement. By exposing the bacteria to gradual cold stress, researchers trigger higher pigment yields as a protective response. For instance, Marín et al., 2022 optimized *Janthinobacterium svalbardensis* for violacein production under prolonged cold adaptation (10°C), leading to enhanced pigment output, and Mukhia et al., 2024 reported that *Zobellia laminarie* exhibited increased carotenoid biosynthesis after undergoing adaptive selection under repeated freezethaw cycles. Metabolic engineering approaches were employed in the study of Silva et al (2019) where they introduced a foreign carotenoid biosynthesis gene into *Streptomyces cyaneus* that led to the enhanced production of hybrid pigments.

The studies conducted by Zeleke et al. (2024) and Wang et al. (2020) used CRISPR-Cas9 genome editing that allows knock-in or knock-out modifications in pigment-producing bacteria. Zeleke et al. (2024) successfully deleted competing metabolic pathways in *Chromobacterium violaceum*, leading to enhanced violacein production, and Wang et al. (2020) used CRISPR to introduce pathway-specific mutations that increased prodigiosin yield in *Serratia marcescens*.

BACTERIAL PIGMENTS AND THEIR PRACTICAL APPLICATIONS

Bacterial pigment research is gaining momentum due to its bioactivity, sustainability, and eco-friendly production methods compared to synthetic dyes. These pigments exhibit diverse functionalities in pharmaceuticals, cosmetics, textiles, food, and biotechnological applications as an alternative to synthetic dyes (Marey et al., 2024).

1. Carotenoids

Carotenoids were among the most frequently identified pigments in the reviewed studies. They are naturally occurring lipophilic tetraterpenoids with long conjugated double bonds, giving them strong antioxidant and photoprotective properties. The extensive polyene structures allow them to absorb light in the blue-green range (~450–570 nm), which gives them vivid yellow, orange, or red colours (Barreto et al., 2023; Aslam et al., 2021). In photosynthetic organisms, they serve as accessory light-harvesting pigments and protect the photosystems from excess light damage by quenching excited chlorophyll and oxygen-free radicals (Moise et al., 2014).

Carotenoids are broadly classified into two groups based on their chemical composition: carotenes and xanthophylls. Carotenes are hydrocarbons, whereas xanthophylls are their oxygenated derivatives (containing oxygen in the form of hydroxyl, carbonyl, or epoxy groups) (Barreto et al., 2023; Aslam et al., 2021). Common carotenoids identified in the review are Bacterioruberin, Zeaxanthin, β-Cryptoxanthin, Decaprenoxanthin, β-Carotene, Lutein, Canthaxanthin, Torulene, Lycopene, and Sarcinaxanthin. Studies identified that these pigments have high commercial relevance due to their antioxidant, UV-protective, and immune-boosting properties, making them valuable for applications in the food, nutraceutical, and cosmetic industries.

2. Phenazines

Phenazines are nitrogen-containing heterocyclic compounds that exhibit antimicrobial properties (Huang et al., 2024). The study identified Pyocyanin, Pyoverdine, and other phenazine derivatives predominantly produced by *Pseudomonas aeruginosa*. These pigments play a role in bacterial virulence but also exhibit potent antibacterial, antifungal, and anticancer properties (Elbargisy et al., 2021; Abdelaziz et al., 2022). Pyocyanin production was optimized through nutrient media modifications and incubation time adjustments, and the purified pigments demonstrated strong biofilm disruption capabilities, making them relevant for wound treatment and antimicrobial textile development (Seo et al., 2024). In another study, Moura et al. (2014) documented phenazine and naphthoquinone (phthiocol) production in *Mycobacterium tuberculosis*. Phenazines are used in biosensors, antimicrobial coatings, and as tools for studying redox biology in microbial ecosystems (Moura et al., 2014).

3. Prodigiosin Group

Prodigiosin is a red tripyrrole pigment with strong antimicrobial, anticancer, and immunosuppressive activity. Structurally, it comprises a linear tripyrrole ring system and is typically produced under aerobic fermentation (Mandal et al., 2023; Jinendiran et al., 2019). *Serratia marcescens*, *Serratia plymuthica*, *Zooshikella sp*., and *Janthinobacterium sp*. were the significant producers of prodigiosin. Studies by Venil et al. (2021) and Amorim et al. (2022) optimized prodigiosin for textile dyeing because it has high stability and binding affinity to textiles, making it a sustainable alternative to synthetic dyes in the textile industry (Mary et al., 2023). The commercial relevance of prodigiosin lies in its vivid red colour, high stability, and bioactivity. Nowadays is gaining traction in natural dye industries, bioelectronics, and anticancer drug development (Mohammad et al., 2024; Pallath et al., 2024).

4. Violacein Group

Violacein is a violet bisindole pigment known for antimicrobial, antiviral, and anticancer properties. Its biosynthetic pathway involves tryptophan derivatives. Studies identified violacein production in *Chromobacterium violaceum*, *Janthinobacterium* sp., and *Pseudoalteromonas rubra* (Sulaiman et al., 2016; Alem et al., 2020). This indole-based pigment has been extensively studied for its antitumor, antifungal, and wound-healing properties. Optimization studies employed UV-light irradiation, pH variations, and agro-waste substrates to enhance violacein production (Ghosh et al., 2020). Due to its high bioactivity and stability, violacein holds potential for applications in pharmaceuticals

5. Melanin Group

Melanins are dark pigments derived from the oxidation of phenolic or indolic compounds, often linked to UV protection, metal ion chelation, and free radical scavenging. Melanin pigments, including pyomelanin, eumelanin, and standard melanin, were found in *Bacillus haynesii*, *Streptomyces torulosus*, *Exophiala crusticola*, and *Mycobacterium tuberculosis*. These pigments are known for their UV-protective, antioxidative, and neuroprotective functions (ElBatal et al., 2017; Wang et al., 2020).

Many studies optimized melanin production by adjusting pH, light exposure, and nitrogen sources (Hosseinpour et al., 2017). El-Batal et al. (2017) and Wang et al. (2020) described high-yield production using gamma radiation, and Bolognese et al. (2019) showed pyomelanin production using recombinant *E. coli*. Melanin's utility in cosmeceuticals, biodegradable UV-protective films, electronic materials (due to its semiconducting properties), and pharmaceuticals is rapidly expanding. Pyomelanin's high antioxidant capacity also lends itself to anti-ageing formulations.

6. Flexirubin-Type Pigments

Flexirubin-type pigments are hydrophobic aryl-polyene esters, typically yellow to orange in color. Their chromophore structure consists of a resorcinol-derived polyene chain conjugated with a phenolic ring. One of the hallmark properties of flexirubin pigments is their pH-dependent color shift—appearing yellow under neutral to acidic pH and turning red-orange in alkaline conditions. Flexirubins are primarily membrane-associated pigments and are believed to play protective roles in bacteria by stabilizing cell membranes, especially under stressful environmental conditions.

Chryseobacterium shigense and *Chryseobacterium sp.* UTM-3T was among the key strains reported to produce flexirubin-type pigments (Amorim et al., 2022). The analysed studies collectively demonstrate that agitation and aeration, combined with carbon source variation, significantly impact pigment yield and chromatic intensity of the pigments. Despite the limited commercial penetration thus far, flexirubin-type pigments hold promise in textile dyeing, food, and cosmetics.

7. Quinones and Naphthoquinones

Quinones are a class of aromatic diketones, while naphthoquinones specifically contain a naphthalene core substituted with quinone groups. These pigments are involved in electron transport and redox cycling in microbial metabolism and are often produced as secondary metabolites with strong bioactivity, including antimicrobial, antifungal, and anticancer effects. Quinones such as quinoline derivatives and naphthoquinones were identified in *Gordonia alkanivorans* and *Stenotrophomonas sp.* (Sarkar et al., 2022). Mandal et al. (2023) isolated quinoline derivatives from *Kocuria indica* RSAP2 isolated from Arctic soil, and Moura et al. (2014) reported phthiocol, a naphthoquinone compound, from *Mycobacterium tuberculosis*, co-produced with phenazines. Phthiocol is structurally related to vitamin K derivatives and exhibits strong antimicrobial activity.

These pigments with strong antimicrobial and antioxidant properties make them ideal candidates for use in biocidal coatings, pharmaceuticals, and industrial biopigments. Optimization approaches included fermentation process tuning and genetic modification techniques to increase yield and stability.

8. Polyketides

Polyketides are structurally diverse natural products biosynthesized by polyketide synthase (PKS) enzymes, which assemble acetate/malonate units into complex molecules. Studies identified aryl polyene/dialkylresorcinol hybrids such as arcuflavins A and B, which represent hybrid polyketides, combining polyene chains and aromatic resorcinol rings (Janković et al., 2023). *Variovorax paradoxus* B4, as reported by Schöner et al. (2016), produced

arcuflavins A and B, yielding up to 93.6 nmol/g dry weight under optimized conditions. This strain was cultured in LB medium, and pigment production was attributed to hybrid biosynthetic gene clusters encoding both aryl-polyene and resorcinol synthesis pathways. This marks an important contribution to the field, as it links environmental bacteria with the production of novel polyketide pigments through combinatorial biosynthesis.
Although optimization studies for these specific polyketides are limited, Schöner et al. highlighted the influence of carbon source availability, culture density, and oxygen levels on pigment yield. Given the complex nature of polyketide biosynthesis, future strategies may involve genetic manipulation of biosynthetic gene clusters and the use of synthetic biology platforms (e.g., *E. coli* chassis) for enhanced yields. Given the versatility and chemical diversity of polyketides and their compatibility with synthetic biology, these pigments represent one of the most promising groups for high-value biotechnological exploitation.

GAPS IN CURRENT RESEARCH AND FUTURE PERSPECTIVES

The studies we analysed demonstrated successful pigment production using bacterial strains, but the pigment production was limited to laboratory-scale. Very few studies translate these findings to pilot or industrial-scale fermentation systems. Most reviewed studies were conducted in shake flasks or 5–10 L bench-scale bioreactors. The transition from bench to bioreactor, especially beyond 1000 L, presents issues related to oxygen transfer, shear stress, foaming, contamination, and cost efficiency. Moreover, parameters optimized at lab scale often behave differently in large-scale systems due to altered hydrodynamics and microbial behaviour (Venil et al., 2014; Silva et al., 2019; Mukhia et al., 2024).

Future studies should focus on scale-up strategies, including bioprocess modelling, scale-down simulation studies, and real-time fermentation control to ensure pigment stability and consistency in larger volumes ((Efimova et al., 2023; Amorim et al., 2022).

As there is a lot of research happening in the domain of bacterial pigments isolation and commercialisation, we also looked into the real-world applications, to check whether any practical large-scale applications were there or not (Zeleke et al., 2024; Elbargisy et al., 2021; Mohammad et al., 2024).

Our first attention was laid upon a UK-based company called Colorifix (2023), which uses engineered microbes to dye fabrics. Interestingly, their bacterial pigments are used by several fashion brands to dye their fabrics. The company claims that the source of the pigment-producing bacteria was from the soil and deep-sea sediments. Their customised pigment-producing bacterial strains and fermentation systems prove the real-world application of these pigments (Colorifix, 2023).

Only a handful of studies evaluate the cost-benefit ratio or techno-economic viability of bacterial pigment production. The lack of cost analysis for substrate use, yield per liter, downstream processing, purification, and pigment stability testing limits our understanding of commercial feasibility. Standardized economic modeling frameworks and life-cycle assessments (LCA) should be applied to bacterial pigment production pipelines. Identifying low-cost feedstocks, such as agro-industrial waste, coupled with cost-effective extraction methods, can bridge this gap. Another France-based biotech company working in the same direction is the Pili (2022), they are using agricultural biomass as a resource and renewable raw material for the production of biobased dyes, through fermentation. Through the integration of synthetic biology and fermentation, they offer bio-based dyes, with a offer of low-carbon direct replacement for petro-based indigo without compromising on scalability and performance in terms of shade, vibrancy and colorfastness, and purity of more than 90%.

Although bacterial pigments show promise in food, cosmetics, and pharmaceuticals, comprehensive safety profiles are lacking. Only a few carotenoids (like β-carotene or lutein) are recognized as GRAS (Generally Recognized as Safe) (Adadi et al., 2018; Rymbai et al., 2011). Pigments like violacein, prodigiosin, and melanin have bioactivity, but their toxicological, allergenic, and metabolic impact on human health has not been thoroughly studied across age groups and exposure durations (Kumar et al., 2015).

Through this systematic review, we have attempted to provide a qualitative condensation of current evidence regarding bacterial pigment research, applications, and challenges as competent industrial raw materials. We used the PRISMA framework and a structured synthesis to facilitate the proper identification of studies and to ensure that the results are reproducible. This is not a commonly adopted approach in other reviews. Adopting the systematic review methodology also helped us focus on the area of interest and reduce the lengthy nature of the review. Even though we followed a scientifically rigorous methodology in this review, certain limitations also need to be acknowledged. The current review only summarizes studies published in the past ten years. Moreover, we only considered studies published in English, which may have excluded relevant research published in other languages. Readers are advised to keep these factors in mind while interpreting the results of this systematic review.

The results of this study will be a valuable summary and guide for ongoing and future research endeavors aimed at exploring bacterial pigments and their properties.

CONCLUSION

The review identifies 84 pigment-producing bacterial species and 24 structurally and functionally diverse pigments classified into eight major groups, including carotenoids, melanin, phenazines, prodigiosin, violacein, flexirubin-type pigments, quinones/naphthoquinones, and polyketides. These pigments exhibit a wide range of applications in pharmaceuticals, cosmetics, textiles, and food industries.

Synthesized evidences suggest that bacterial pigments are not only a subject of academic interest but are also being integrated into real-world applications. To fully realize the commercial and ecological benefits of bacterial pigments, future research must embrace a multidisciplinary outlook. Emphasis should also be placed on the development of standardized protocols, economic modeling, biosafety assessments, and pilot-scale demonstrations. By compiling and analyzing this body of work, our review aims to serve as a guide for future research and innovation in bacterial pigment research.

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