



## Review

# Antioxidants: Mechanisms, Benefits, and the Importance of Extremophilic Microorganisms

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## Abstract

Despite their vital physiological roles, oxidative imbalance caused by reactive oxygen, nitrogen, sulphur, and chlorine species damages essential body macromolecules such as proteins, lipids, and nucleic acids through oxidative stress. This stress is strongly associated with cancer, inflammation, neurological and cardiovascular disorders, and other chronic human diseases. Therefore, antioxidants, natural or synthetic, that counteract oxidative damage are important, with increasing interest in their use within the pharmaceutical, food, and cosmetic industries. However, due to toxicity concerns with the synthetic variants, natural antioxidants are increasingly preferred. Extremophile-derived antioxidants, such as superoxide dismutases, catalases, peroxidases, carotenoids, and melanin, are of renewed interest due to their remarkable stability, robustness, and potency under extreme conditions of temperature, pH, and salinity. These make them better than many mesophile-derived antioxidants and excellent candidates for cost-effective biotechnological, research, and industrial processes that require high operational efficiency. This review summarises key classes of selected enzymatic and pigment antioxidants, their mechanisms of action, and their industrial relevance, with a focus on extremophilic microalgae, bacteria, and fungi. The benefits of extremophilic antioxidants are discussed alongside their current applications and existing challenges, including the need to develop efficient delivery systems, scalability issues, and limited characterisation.

**Keywords:** oxidative stress; carotenoids; extremophilic microorganisms; industrial applications; antioxidants

## 1. Introduction

Reactive species such as reactive oxygen species (ROS), reactive sulphur species (RSS), reactive chlorine species (RCS), and reactive nitrogen species (RNS) play key roles in human physiological functions such as cell signalling, immunity, and gene regulation [1,2] and the development of some diseases [3,4]. Reviews of the literature indicate that ROS and other reactive species induce oxidative stress, damaging macromolecules such as proteins, carbohydrates, lipids, and DNA. This damage is thought to contribute to the development of different diseases such as cancer, asthma, cardiovascular problems, arthritis, autoimmune disorders, and neurological problems, including Parkinson's dementia [2,5]. Substances or compounds that slow down or inhibit the free radical-mediated oxidation of these body macromolecules are called antioxidants [6]. These function by reducing the levels of available reactive species through scavenging, dismutation, and degradation into harmless molecules to mitigate their oxidative damage potential [4].



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Antioxidants can be natural or synthetic [4,7]. Natural forms of antioxidants are either exogenous or endogenous. Exogenous antioxidants are those sourced from outside the body, typically through the consumption of plant-based food, herbs, and spices. These include vitamins (e.g., ascorbic acids, vitamins C and E), minerals (e.g., Selenium, copper, manganese, and zinc), carotenoids (e.g.,  $\alpha$  and  $\beta$ -carotene, lutein, and lycopene), and polyphenols (e.g., flavons, anthocyanins, and phenolic acids) [3,8]. In contrast, endogenous antioxidants are produced naturally in the body via enzymatic and non-enzymatic means. Examples of enzymatic antioxidants include enzymes such as catalase, superoxide dismutase (SOD), and glutathione reductase [8], while low molecular weight compounds such as lipoic acids (lipophilic) and uric acids (hydrophilic), and metal-binding albumin are examples of non-enzymatic antioxidants. Extensive information on the different types of antioxidant systems, sources, mechanisms of action, and potential uses is available [1,4,9].

Synthetic antioxidants are artificial and include recombinant SODs, phenolics, nano-antioxidants (metallic nanoparticles and antioxidant-functionalised nanoparticles), nitrones/nitroxides, iron-ion chelators, and synthetic oxidases [3,4,10]. However, some commonly used synthetic phenolic antioxidants, such as butylated hydroxyanisole (BHA), butylated hydroxytoluene (BHT), and tertiary butylhydroquinone (TBHQ), have been linked to significant adverse health effects, including cytotoxicity, carcinogenicity, and endocrine disruption, making their use controversial [10]. However, due to the observed toxicity, there is increasing interest in the use of antioxidants from natural or biological sources, as these are less toxic, cheaper, and show comparative or greater efficacy than synthetic antioxidants [11,12]. Therefore, this review provides a brief overview of the mechanisms of action of natural and synthetic antioxidants. Thereafter, it focuses on extremophilic microalgae, bacteria, archaea, and fungi as current and emerging sources of robust natural antioxidants, including superoxide dismutases, catalases, peroxidases, carotenoids, and melanin, highlighting their advantages over conventional organisms. The current and potential applications of extremophile-derived antioxidants in the different fields, such as pharmaceutical (medical), food, and industrial sectors, are evaluated alongside existing challenges and research gaps to overcome for broader industrial application.

This review is novel compared to most recent reviews in multiple ways. With respect to scope and coverage, this review treats bacteria, archaea, fungi, and microalgae from different environments as coequal sources of extremophilic antioxidants. This is in contrast to some other reviews or reports that are exclusively focused on antioxidants from a specific group, such as bacteria [13,14], archaea [15], fungi [16], microalgae [17–19], or specific genus/species or environment [20]. Therefore, the review presents a cross-kingdom antioxidant–extremophile perspective that allows for ease of comparison and identification of cross-kingdom antioxidants, which is not possible with a single group (e.g., microalgae-only) review. Additionally, while most recent reviews or reports on antioxidants from biological systems are usually limited to one or two sectors (e.g., food or cosmeceuticals) [21,22], this review presents the application of extremophile-derived antioxidants such as SODs, catalases, and carotenoids across *multiple* sectors: food/packaging and preservatives, medicine/pharmaceuticals, cosmetics, textile and manufacturing, and environmental bioremediation. It uniquely identifies gaps in knowledge, delivery challenges, and current industrial applications. Other known antioxidants, such as vitamins E and C, exopolysaccharides, and ectoines, have not been reviewed in this paper.

## 2. Mechanisms of Action of Antioxidants

Antioxidants, whether synthetic or natural, can be categorised into primary antioxidants and secondary antioxidants based on their modes of action. Primary antioxidants directly reduce or inhibit the oxidative processes associated with the reactive species,

while secondary antioxidants act indirectly on the oxidative processes [23]. They do this through different means, with primary antioxidants scavenging acting as oxygen scavengers through chain breaking and atom/electron donations, while secondary mechanisms include metal ion chelation, inhibition of peroxides, and singlet oxygen elimination [23,24]. Free radical scavenging is a key mechanism of antioxidant activities. Antioxidants carry this out via two mechanisms: the donation of hydrogen atoms, hydrogen-atom transfer (HAT), or electrons or single-electron transfer (SET) to free radicals, thereby stabilising them before they propagate and initiate oxidative actions [24]. Another mechanism is the use of endogenous enzymatic systems such as superoxide dismutase (SOD), catalase (CAT), and peroxidases to detoxify reactive species. SOD detoxifies oxidants by converting superoxide radicals into hydrogen peroxide and molecular oxygen, while CAT converts hydrogen peroxide into water and oxygen. Other enzymes, such as peroxidases (e.g., glutathione peroxidase, ascorbate peroxidases, and peroxiredoxins), can also detoxify ROS. For example, glutathione peroxidase catalyses the detoxification of hydrogen and lipid peroxides by using reduced glutathione (GSH) to convert these reactive species to water or corresponding alcohols, thereby protecting cells from oxidative damage [25]. Some other antioxidants function through the repair of oxidatively damaged proteins, reversing the effects of the oxidative damage to cells. A good example is methionine sulfoxide reductase. Methionine sulfoxide reductase (Msr) is an example of an antioxidant that repairs damaged or oxidised macromolecules [26]. Msr acts by reversing the reactive species-induced oxidation of methionine residues by catalysing the reduction of methionine sulfoxide back to methionine, thereby restoring protein function and stability [27]. Metal chelation is another mechanism of action of some antioxidants. Metal ions such as  $\text{Cu}^{2+}$  and  $\text{Fe}^{2+}$  can catalyse the generation of reactive hydroxy species, which damage cells. Antioxidants, such as flavonoids (polyphenols), can chelate or bind these metal ions, inhibiting the generation of these free radicals and limiting cellular damage [28]. Other mechanisms, such as the quenching of singlet oxygen formation by carotenoids to prevent ROS activity and antioxidant regeneration to maintain a protective pool, are known [25,29] (Figure 1).

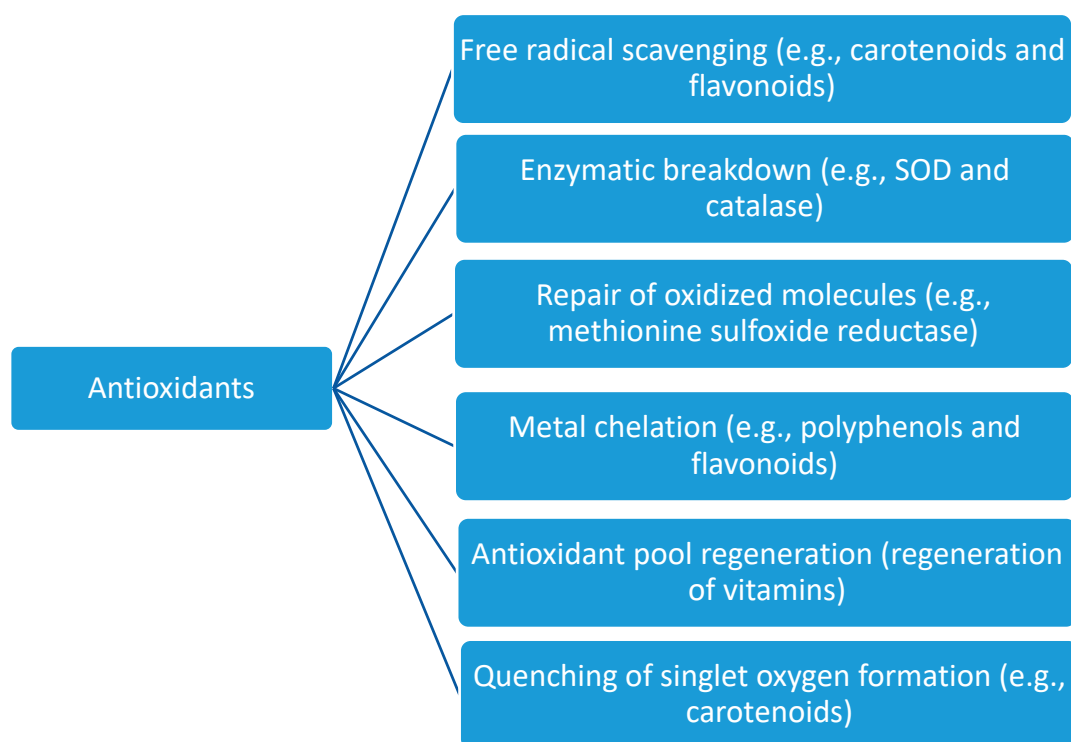


**Figure 1.** Mode of action of antioxidants.

Singlet oxygen molecules are highly reactive excited states of oxygen that can cause oxidative stress in cells. Singlet oxygen quenching by some antioxidants neutralises oxidative activities, and this can occur via physical quenching or absorption of excitation energy by antioxidants (non-reactive energy transfer), such as carotenoids [30]. It can also occur through chemical quenching, which is when the excited molecules react with antioxidants such as phenols, ascorbic acids, and polyphenols to form non-oxidative compounds [31,32]. Antioxidant regeneration refers to when a primary antioxidant, which is in a reduced state/activity (oxidised state) after neutralising the reactive species, is restored to its functional state and original activity by a secondary antioxidant [33].

### 3. Importance of Antioxidants

Antioxidants have many benefits; however, for this review, the focus will be on their health and industrial benefits using the food industry as a case study.

Antioxidants, whether endogenous or exogenous, can benefit human health. This is because they constitute a line of mutually supportive defence necessary for maintaining the oxidant/antioxidant balance in the body, with associated health benefits [34]. Some natural antioxidants may enhance the efficacy of cancer therapy and reduce toxicity [35] and bladder cancer risks [36]. Reductions in blood pressure, enhanced insulin sensitivity, improvement in eye sight, skin disease treatments, and cardiovascular outcomes in trials involving the application of different antioxidants such as lycopene, astaxanthin, lutein,  $\beta$ -carotenes, and canthaxanthin are known [18,37–39]. Unfortunately, human beings are unable to synthesise these carotenoids; therefore, they are diet-derived [40,41]. A review of the literature by [42] has shown that plant-sourced phenolic compounds, such as anthocyanins, flavonols, flavones, and phenolic acids, found in dairy products (such as milk and cheese), animal feeds, or added as additives, enhance their nutritional profile and confer multiple health benefits, including antidiabetic, cardioprotective, neuroprotective, and anticancer properties. There are excellent reviews on the use of antioxidants as nutraceuticals and pharmaceuticals [43,44].

Antioxidants are beneficial to the food industry, where they can be used to extend the shelf-life of food products via inhibition of adverse oxidative processes or their potential incorporation in food packaging in active packaging and to maintain and improve the sensory, nutritional, and health profiles of these products. For example, natural antioxidants such as olive biphenols can be used to extend the shelf lives of beef, pork, and fish products by reducing the rate of lipid oxidation (up to 83%), preserving vitamin and omega-3 levels, thereby maintaining the organoleptic properties of these foods [45]. Similarly, terpenoids (monoterpenes, carotenoids), polyphenols (phenolic acids, flavonoids, lignans), lignin/nanolignins from plants have been shown in various studies to preserve and/or extend the shelf life of meat and fish products when added as additives or into the packaging matrix, as in the case of lignin [46–48]. Other reviews have shown that the antimicrobial and antioxidant properties of the phenolic components of essential oils have been utilised to maintain the quality and shelf lives of meat, fruits, and vegetables [49].

Other benefits of antioxidants include their use in creams and topical application to protect the skin from oxidative and UV damage (anti-ageing, photoprotection) [50]. They have also been used as nutritional supplements to improve the yield (weight gain) of fish in aquaculture [51,52]. Antioxidants have also been used in the textile industry and as stabilised enzymes in research activities [53].

### 4. Sources of Natural Antioxidants

Given the challenges associated with synthetic antioxidants, naturally occurring antioxidants with lower toxicity are preferable, and this is the focus of this review. Natural

antioxidants can be a natural component of the living system or introduced into the system via diet, usually through food and supplements, with these antioxidants invariably derived from living systems such as plants, animals, and microorganisms [4]. Natural antioxidants have been obtained from or demonstrated in bacteria [54], fungi [14], fruits, vegetables, and plants in general [55]. While comprehensive reviews of antioxidants with respect to their sources, types, mechanisms, and applications from natural and synthetic sources abound [1,4,25], limited information on these antioxidants from a special group of biological systems, extremophilic systems, is available.

## 5. Extremophiles as a Source of Antioxidants

Extremophilic biological systems (microorganisms) are a rich source of stable antioxidants due to their evolutionary adaptation to surviving in extreme conditions, such as those of temperature, acidity, and salinity, compared to those from conventional biological systems [18,56,57]. This is a key advantage as extremophiles produce structurally stable and robust antioxidants (enzymes) that can maintain their functionality under conditions that would have adversely affected antioxidants from other sources. Additionally, some of these antioxidants are unique and often have superior catalytic activities compared to antioxidants from other sources [20]. Therefore, high-value robust and potent antioxidants such as phenolics, specialised enzymes, carotenoids, and rare biomolecules with elevated oxidative capacities, are prime candidates for industrial exploitation [18,19,58–60]. Consequently, they are potentially suitable for different industrial and biotechnological applications in the food, cosmetic, and pharmaceutical sectors. Using enzymes from extremophilic organisms for industrial purposes offers important operational benefits. The ability of extremophiles to grow under extreme environmental conditions, such as extremes of temperature, salinity, and pH (inhibitory to most microorganisms), helps minimise contamination risks by other microbial groups. This reduces operational costs, improves process efficiency and stability, particularly when employed in large-scale industrial cultivation and production systems [18,19]. Therefore, this intrinsic stability under harsh conditions should offer a clear competitive advantage over conventional biological sources. Therefore, extremophilic systems are expected to be able to sustain the required efficiency for antioxidant biosynthesis and yield improvement during industrial operations. Consequently, antioxidants derived from extremophilic biological systems should attract significant scientific and industrial interest and, when available, could be preferred to those derived from conventional sources, especially if stress-adapted antioxidant generation pathways are optimised for greater yield. Some of the different types of extremophiles, such as acidophiles, alkaliphiles, barophiles, psychrophiles, halophiles, and radiophiles, are known (Table 1) [61,62].

**Table 1.** The Different Types of Extremophilic Microorganisms.

| Designation  | Extreme Conditions                                   | Habitat and Examples                                                                                                                                                                                                   |
|--------------|------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Acidophiles  | Acid-loving. Grows at a pH below 5. Optimum pH is 3. | Hydrothermal vents, mine sites, and geothermal acidic sites. Examples include <i>Acidithiobacillus thiooxidans</i> and <i>Acidithiobacillus thiooxidans</i> [61,63].                                                   |
| Alkaliphiles | Alkali-loving. Grows at pH 9 and above.              | Manufacturing effluent, mining operations, paper and pulp production, and alkali lakes. Examples include <i>Bacillus</i> sp., <i>Acremonium</i> , and <i>Sodiomyces</i> species [61,64,65]                             |
| Capnophiles  | Grows at a CO <sub>2</sub> concentration of 1–10%.   | Clinical samples (urine of patients with severe pyelonephritis) and cold-water geysers. Examples include <i>Lactobacillus</i> , <i>Proteus mirabilis</i> , <i>Streptococcus pneumonia</i> , and <i>E. coli</i> [61,66] |

Table 1. Cont.

| Designation   | Extreme Conditions                                  | Habitat and Examples                                                                                                                                                                                         |
|---------------|-----------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Halophiles    | Salt-loving. Grows at 1.5–4.0 M salt concentrations | Salt lakes, marshes, and ponds, and manufacturing effluents. Examples include <i>Haloquadratum walsbyi</i> , <i>Dunaliella</i> sp., and <i>Actinarchaeum halophilum</i> [61,67]                              |
| Metallophiles | High metal concentration-loving                     | Manufacturing effluent, mine tailings, mine sites, contaminated groundwater, and aquifers. Examples include <i>Acinetobacter</i> , <i>Citrobacter</i> , <i>Pseudomonas</i> , and <i>Thiobacillus</i> [61,68] |
| Piezophiles   | Pressure-loving, up to 80 MPa                       | Deep-sea environments, underground water. Examples include <i>Salinimonas sediminis</i> , <i>Colwellia marinimaniae</i> , and <i>Shewanella benthica</i> [61,69]                                             |
| Psychrophiles | Cold-loving, grows from −20° to 20 °C               | Arctic and Antarctica, permafrost, deep-sea, and cold storage facilities. Examples include <i>Alcaligenes</i> , <i>Achromobacterium</i> , <i>Alteromonas</i> , and <i>Colwellia</i> sp. [61,68]              |
| Radiophiles   | Radiation-loving, 1500–6000 Gy                      | Nuclear waste, ionised products. Examples include <i>Deinococcus radiodurans</i> [61,70]                                                                                                                     |
| Thermophiles  | High temperature-loving, grows from 46 °C to >75 °C | Hot springs, geysers, manufacturing effluents, and deserts. Examples include <i>Thermus</i> , <i>Bacillus</i> , and <i>Geobacillus</i> sp. [61,71]                                                           |
| Xerophiles    | Dry habitat-loving                                  | Deserts and any other dry environments. Examples include <i>Aspergillus penicillioides</i> and <i>Xeromyces bisporus</i> [61,72]                                                                             |

Note: Adapted from [61].

### 5.1. Sources of Extremophilic Antioxidants: Microalgae

Microalgae are a diverse group composed of photosynthetic prokaryotic and eukaryotic microorganisms, rich in lipid and other biomolecules, which are found in aquatic and terrestrial environments [73–75]. As photosynthetic microorganisms, they convert water, carbon dioxide, and inorganic salts into biomass by using sunlight as an energy source [17]. Extremophilic microalgae are characterised by their ability to grow under extremely acidic or alkaline pH, very high and very low temperatures, and extremes of CO<sub>2</sub>, salts, and metal concentrations [76–78].

Extremophilic microalgae are excellent sources of various robust antioxidants, including SODs, carotenoids, and other antioxidant systems. Extremophilic red microalga *Cyanidioschyzon merolae* (Rhodophyta) from sulfuric hot springs is both a thermophile, growing at temperatures of up to 56 °C, and an acidophile that is nickel resistant under laboratory conditions [78–80]. The adaptive laboratory evolved microalga has a lower amount of ROS compared to the wild type due to the high activity of its Ni-SOD [78]. Sulphur starvation of the extremophilic microalgae *Galdieria sulphuraria* (Rhodophyta) has been shown to induce SOD as an antioxidant to combat nutrient stress [81]. SOD levels were observed to dramatically increase in snow algae *Chloromonas nivalis* (Chlorophyta) when stressed at 4 °C under laboratory conditions, suggesting that this antioxidant system contributed to ROS removal in this organism [82]. Genes coding for SODs have also been observed in halo-tolerant *Dunaliella salina* (Chlorophyta) (a well-known carotenoid-producing algae) under low salinity [83].

Acidophilic algae, such as *Coccomyxa onubensis* (Chlorophyta), have been shown to tolerate high heavy metal concentrations/stress (Arsenic, cadmium, mercury, and copper) through three different antioxidant mechanisms: the ascorbate peroxidase (APX), catalase (CAT), and glutathione reductase systems [84]. Under stressful conditions, most extremophilic microalgae use multiple antioxidative systems. For example, in snow algae, *Chloromonas nivalis* and other microalgae such as *Dunaliella salina* and *Galdieria sulphuraria* are also known to use the catalase system alongside the SOD [82].

Carotenoids and pigments are antioxidants that are produced by extremophilic microalgae in laboratory-based assays and in the natural environment. Thermoacidophilic red alga *Galdieria sulphuraria* found in acidic hot springs (can grow at 56 °C and at low pH) [85] is known to produce a phycocyanin, with proven antioxidant activities through HAT and SET, with the pigment used as a natural colourant in the food industry [24]. *Sanguina aurantia* and *Sanguina nivaloides* (Chlorophyta) found in arctic and subarctic regions produce astaxanthin [86]. *Chromochloris zofingiensis* also synthesises carotenoids such as canthaxanthin and astaxanthin [87]. *Coccomyxa melkonianii* SCCA 048 (heavy metal resistant) is known to synthesise significant amounts of lutein (up to 80% of total carotenoid) [88] while acidophilic *Coccomyxa onubensis* and *Chlamydomonas acidophila* can produce  $\beta$ -carotene and lutein [89–91]. *Deinococcus xibeensis* R13 (radiation- and UV-resistant extremophile) produces Deinoxanthin-type carotenoids (xanthophylls) in significant amounts [92].

Literature reviews have shown that other extremophilic groups, such as *Dunaliella salina* ( $\beta$ -carotene production), *Arthrospira platensis* (c-phycocyanin), *Tetradismus dissociates* (Chlorophyta) (canthaxanthin production), and *Haematococcus lacustris* (formerly *Haematococcus pluvialis*) (Chlorophyta) (astaxanthin production), all have beneficial antioxidants [19,93]. A review of the literature by [18] has shown that extremophilic *Tetradismus dissociates* MT1 (from the Sahara desert) and halophilic/tolerant *Chromochloris zofingiensis* (Chlorophyta) use canthaxanthin as their preferred antioxidant system. Psychrophilic microalgae such as *Scenedesmus* sp. (Chlorophyta), *Chlorococcum* sp. (Chlorophyta), and halophilic *Dunaliella* sp. (Chlorophyta) also produce antioxidative compounds such as lutein, carotene, and antheraxanthin [94,95]. A summary of some of these examples is presented in Table 2.

**Table 2.** Diversity of extremophilic microorganisms and their antioxidant systems.

| Organism (Group)                                | Extremophilic Trait                        | Major Antioxidants                      | Functional Role/Mechanism                                                     | References |
|-------------------------------------------------|--------------------------------------------|-----------------------------------------|-------------------------------------------------------------------------------|------------|
| <i>Cyanidioschyzon merolae</i> (Rhodophyta)     | Thermoacidophile; Ni-resistant             | Ni-SOD                                  | Reduced ROS via enhanced SOD activity in evolved strains                      | [78–80]    |
| <i>Galdieria sulphuraria</i> (Rhodophyta)       | Thermoacidophile; nutrient stress-tolerant | SOD, catalase, phycocyanin              | SOD induced under sulphur starvation; ROS detoxification; pigment antioxidant | [81,85]    |
| <i>Chloromonas nivalis</i> (Chlorophyta)        | Psychrophile                               | SOD, catalase                           | Increased SOD activity at low temperature for ROS removal                     | [82]       |
| <i>Dunaliella salina</i> (Chlorophyta)          | Halotolerant                               | SOD, $\beta$ -carotene                  | SOD gene expression; carotenoid antioxidant system                            | [19,83,93] |
| <i>Coccomyxa onubensis</i> (Chlorophyta)        | Acidophile; heavy metal tolerant           | APX, CAT, glutathione reductase, lutein | Detoxification via multiple antioxidant pathways                              | [84,89–91] |
| <i>Chromochloris zofingiensis</i> (Chlorophyta) | Halotolerant                               | Canthaxanthin, astaxanthin              | Carotenoid-mediated ROS scavenging                                            | [18,87]    |
| <i>Sanguina aurantia</i> / <i>S. nivaloides</i> | Psychrophile                               | Astaxanthin                             | UV and oxidative stress protection                                            | [86]       |
| <i>Coccomyxa melkonianii</i>                    | Heavy metal resistant                      | Lutein                                  | High carotenoid accumulation                                                  | [88]       |

Table 2. Cont.

| Organism (Group)                                                | Extremophilic Trait       | Major Antioxidants              | Functional Role/Mechanism                   | References   |
|-----------------------------------------------------------------|---------------------------|---------------------------------|---------------------------------------------|--------------|
| <i>Thermus thermophilus</i>                                     | Thermophile/halophile     | SOD, catalase                   | Thermostable antioxidant enzymes            | [96,97]      |
| <i>Halomonas</i> sp. ANT108                                     | Psychrophile              | Cu/Zn SOD                       | Cold-active antioxidant enzyme              | [98]         |
| <i>Acinetobacter</i> sp.                                        | Cold/desert extremophile  | Catalase (KatE1)                | Broad pH and temperature activity           | [99]         |
| <i>Serratia</i> sp.                                             | Psychrophile              | Catalase                        | UV-C-resistant catalase                     | [100]        |
| <i>Halobacterium salinarum</i>                                  | Halophile                 | C50 carotenoids                 | Strong antioxidant activity                 | [101]        |
| <i>Haloterrigena turkmenica</i>                                 | Halophile                 | C50 carotenoids                 | Oxidative stress protection                 | [102]        |
| <i>Deinococcus radiodurans</i>                                  | Radioresistant            | Deinoxanthin, SOD, Mn-complexes | Radiation protection and DNA repair         | [20,103–106] |
| Cyanobacteria (e.g., <i>Nostoc</i> , <i>Chroococcidiopsis</i> ) | UV tolerant               | Scytonemin, MAAs, carotenoids   | UV absorption and ROS scavenging            | [107–111]    |
| <i>Phormidium</i> sp.                                           | Psychrophile              | MAAs, carotenoids               | UV protection                               | [112]        |
| <i>Aspergillus fumigatus</i> / <i>Penicillium rubens</i>        | Antarctic fungi           | Catalase                        | ROS detoxification                          | [113,114]    |
| <i>Aspergillus glaucus</i>                                      | Extremophilic fungus      | SOD, catalase                   | ROS scavenging                              | [115]        |
| <i>Cryomyces antarcticus</i>                                    | Polyextremophile          | DHN-melanin                     | Protection against UV, ROS, and desiccation | [116,117]    |
| <i>Exophiala dermatitidis</i>                                   | Polyextremotolerant yeast | DHN-melanin                     | Stress protection                           | [118]        |
| <i>Knufia petricola</i>                                         | Cold-adapted fungus       | Carotenoids                     | ROS scavenging                              | [119]        |
| <i>Dioszegia patagonica</i> / <i>Fusarium</i> sp.               | Cold/halophilic fungi     | Carotenoids                     | Oxidative stress protection                 | [120–124]    |

### 5.2. Sources of Extremophilic Antioxidants: Bacteria and Archaea

An excellent review by [96] has identified an antioxidant system, the superoxide dismutases (SOD), from extremophilic bacteria, which are more stable than SOD from other sources. These SOD are enzymes that can convert toxic superoxide radicals into hydrogen peroxide and oxygen, thus protecting bacterial cells from free radical-induced damage [2]. Enzymes such as catalase or glutathione peroxidase can further break down hydrogen peroxide into water and oxygen [2,125]. For example, *Thermus thermophilus* HB27, originally isolated from a natural hot spring in Japan, is a thermophilic and halophilic bacterium that expresses its antioxidative properties via a robust superoxide dismutase (SOD) that is highly stable at 90 °C [96,97]. Manganese-dependent SODs (active at up to 80 °C and a pH range of 3.0–12.0) have been observed in extremophilic *Bacillus subtilis* (Firmicutes) and *Thermus thermophilus* (Deinococcota) [2].

Other SODs have been reported in the extremophilic *Acinetobacter* sp. (Proteobacteria) [126] and thermoacidophilic *Alicyclobacillus* sp. (Firmicutes) [127]. Conversely, cold-adapted SODs are also known; a good example is the Cu/Zn SOD found in a recombinant

strain, *Halomonas* sp. (Proteobacteria) ANT108, derived from the extremophilic sea-ice strain *Halomonas* sp. [98]. However, the optimum temperature for SOD activity was 35 °C, with 13.9% activity at 0 °C [98]. Fe/Mn SOD has been characterised in *Bacillus licheniformis* (Firmicutes) [128] and Fe SOD in *Thermobifida fusca* (Actinobacteria) [129].

Another antioxidant system encountered in extremophilic bacteria is the catalase system [96]. Excess hydrogen peroxide and hydroxyl radicals can be harmful to cells, with this damage mitigated by catalases, which, as previously stated, can convert these compounds into water and oxygen. A cold-adapted heme catalase system, KatE1, has been identified in an extremophilic *Acinetobacter* (Proteobacteria) isolate from the Atacama Desert plateau (characterised by high UV radiation, salinity, and extremes of temperature) in Argentina [99]. This catalase system was active at up to 50 °C (maximum activity) in laboratory-based assays with “nearly unchanged specific activities” from pH 5.5 to 11 and 0 °C to 40 °C [99]. Similarly, a psychrophilic *Serratia* sp. (Proteobacteria) with a highly stable and thermoactive UV-C-resistant catalase system has been isolated from Elephant Island, in Antarctica [100]. Remarkably, this catalase was active between 20 and 70 °C, with optimal activity at 50 °C and pH 7.0 [100]. Reviews of the literature by [96] have identified different catalase systems, such as a thermophilic Mn-catalase (active at 75 °C and a pH of 9.0) from *Geobacillus* sp. (Firmicutes) strain WCH70, a thermoalkali-stable heme catalase (active at 90 °C) from *Thermus brockianus* (Deinococcota), and a psychrophilic catalase system (0 and 10 °C) from *Aliivibrio salmonicida* (Proteobacteria). Hyperthermophilic archaea such as *Methanosarcina barkeri*, *Methanobrevibacter arboriphilus*, and *Halobacterium halobium* (Euryarchaeota/halobacteriota) are also known to produce catalases [15].

Additionally, carotenoids with higher antioxidant activity than those from conventional sources, such as blueberries and carrots, have been reported in halophilic groups. Laboratory-based assay of carotenoids from *Halobacterium salinarum* (an archaeon) showed that antioxidant activities from this extremophile were almost 2-fold higher than those of carotenoids from berries [101]. Carotenoids have also been obtained from an extremophilic *Arthrobacter* sp. (Actinomycota) [103]. Similarly, halophilic *Haloterrigena turkmenica* (Euryarchaeota), an extremophilic archaeon, is known to mainly secrete C50 carotenoids to protect it from oxidative species in laboratory-based assays [102]. In general, hyperthermophilic archaea use a variety of catalases, SOD, and peroxiredoxins to scavenge destructive ROS in the environment [15]. Furthermore, radioresistant *Deinococcus radiodurans* (Deinococcota) is well known for its utilisation of antioxidant proteins, low molecular weight manganese complexes, and carotenoids (deinoxanthin) [20,103–105] and a Cu/Zn SOD system [106] to protect it from ionising radiation and to repair radiation-induced DNA damage. Similarly, extremophilic halophiles, *Halococcus morrhuae* (Euryarchaeota), *Halobacterium salinarum* (Euryarchaeota), and the bacterium, *Thermus filiformis* (Deinococcota), are also known to produce carotenoid groups [130].

Cyanobacteria are another bacterial group that is known to produce antioxidants. Extremophilic cyanobacteria can be classified as psychrophiles, alkaliphiles, thermophiles, xerophiles, and halophiles based on their habitat [131]. These groups can produce potent and robust UV-absorbing antioxidant compounds such as scytonemin and mycosporine-like amino acids alongside other commonly known antioxidants like SODs, catalase, and carotenoids as adaptations to their harsh growth environments. Scytonemin (pigments) and mycosporine-like amino acids (MAAs) are produced by cyanobacteria to protect themselves from the oxidative stress associated with ultraviolet (UV) radiation, enabling them to survive in different environments, including those characterised by UV radiation, temperature extremes, and low water activity [107].

Cyanobacterium *Nostoc* (Cyanobacteriota) commune Vaucher ex Bornet et Flahault, isolated from Antarctica, has been shown to produce substantial levels of scytonemin for

UV-associated oxidative stress reduction [108]. Others, such as *Leptolyngbya* cf. *fragilis* (Cyanobacteriota), were isolated from a hot spring [109], endolithic *Halotheca* (Cyanobacteriota) cyanobacteria from the Atacama Desert [110] and *Chroococcidiopsis* sp. (Cyanobacteriota). UAM571 [111] also isolated from the same desert were found to produce increasing levels of scytonemin under stress. Substantial levels of UV-protecting mycosporine-like amino acid (MAA) and carotenoids had been identified in *Phormidium* sp. (Cyanobacteriota) isolated from Antarctica [112]. *Aphanotheca halophytica* (Cyanobacteriota), a halotolerant cyanobacterium that produces mycosporine-2-glycine, has been isolated from Solar Lake in Sinai [19]. A summary of some of these examples is presented in Table 2.

### 5.3. Sources of Extremophilic Antioxidants: Fungi

Like other reviewed biological systems, extremophilic fungi utilise standard antioxidant systems, which can be enzymatic (e.g., superoxide dismutases, peroxiredoxins, and catalases) or non-enzymatic (e.g., carotenoids and melanin). These systems scavenge ROS and neutralise free radicals. As reported for microalgae and bacteria, these systems enable them to survive habitat-related stressors, such as extremes of temperature, either very hot, like in the desert, or very cold, as in Antarctica, extremes of pH, low water activities/drought, metal toxicity, high salinity, and high radiation [132]. A brief review of reported examples of extremophilic fungi and their antioxidant systems is presented in the following paragraphs, with relevant references.

Catalase systems have been identified in Antarctic *Aspergillus fumigatus* (Ascomycota) [113], *Penicillium rubens* [114], and *Aspergillus glaucus* (Ascomycota), with the latter having a functional ROS-scavenging SOD [115]. A comprehensive review of other enzymatic antioxidant systems, such as peroxiredoxins, thioredoxins, and glyoxalases, has been carried out [133].

Melanin, a pigment, is known to be one mechanism by which some extremophilic fungi protect themselves from oxidative damage [120]. Different types of melanin have been identified in extremophilic fungi. These include DHN melanin (1,8-Dihydroxynaphthalene) (allomelanin), pyomelanin, and L-DOPA-melanin (L 3,4-dihydroxyphenylalanine) (Eumelanin/pheomelanin), with DHN and L-DOPA melanin being commonly associated with fungi belonging to the basidiomycetes and the ascomycetes [134,135]. Both eumelanin and allomelanin exhibit strong antioxidant properties via well-studied mechanisms. Both can scavenge free radicals such as DPPH (1,1-diphenyl-2-picrylhydrazyl) and ABTS (2,2'-azino-bis(3-ethylbenzothiazoline-6-sulfonic acid)), which are involved in ROS and UV radiation and redox cycling [136–140]. While there is sometimes metabolic flexibility with both pathways existing in some fungal genera, such as *Cryomyces antarcticus* [116], it appears that, in general, the basidiomycetes primarily produce eumelanin using tyrosine-dependent pathways, while ascomycetes largely synthesise allomelanin using a different pathway, such as the polyketide pathway [141,142].

Antarctic black fungus *Cryomyces antarcticus* (Ascomycota) is an example of a fungus that is known to produce this pigment, which protects it from the oxidative effects of temperature stress, UV radiation, and desiccation [116,117]. *Exophiala dermatitidis*, a polyextremotolerant yeast, is also known to synthesise DHN melanin [118]. Melanin is also known to protect black yeasts, which are commonly found in hypersaline conditions [121,143].

Carotenoids have also been reported in cold-adapted *Knufia petricola* A95 [119] and in other extremophilic fungi such as *Dioszegia patagonica* (Basidiomycota) and Antarctic *Arthrobotrys* sp. (Ascomycota) [120,122,123] and in some halophilic *Fusarium* sp. (Ascomycota) [121,124]. Other compounds, such as phenols, xanthenes, anthraquinones, and alkaloids, which scavenge ROS, have been reported in Antarctic fungi [9]. A summary of some of these examples is presented in Table 2.

## 6. Applications of Antioxidants from Extremophilic Microorganisms

Antioxidants such as superoxide dismutases (SODs), catalases, and carotenoids, obtained from extremophilic biological systems, have various applications owing to their stability and their ability to combat oxidative stress. Some of these applications (current and potential) are presented in the following paragraphs and summarised in Table 3.

**Table 3.** Commercial antioxidant products derived from extremophiles.

| Product/Compound                    | Commercial Product Name | Manufacturer                                 | Source Organism                          | Extremophile Type               |
|-------------------------------------|-------------------------|----------------------------------------------|------------------------------------------|---------------------------------|
| $\beta$ -carotene                   | Betatene®               | BASF (Fargo, ND, USA)                        | <i>Dunaliella salina</i>                 | Halophilic microalga            |
| Astaxanthin                         | BioAstin®               | Cyanotech Corporation (Kailua-Kona, HI, USA) | <i>Haematococcus pluvialis</i>           | Stress-tolerant microalga       |
| Phycocyanin                         | LinaBlue®               | DIC Corporation (Irvine, CA, USA)            | <i>Arthrospira platensis</i> (Spirulina) | Alkaliphilic cyanobacteria      |
| Mycosporine-like amino acids (MAAs) | Helioguard® 365         | Mibelle Biochemistry (Buchs, Switzerland)    | Red algae/cyanobacteria                  | UV-resistant extremophiles      |
| Ectoine                             | Ectoin®                 | Bitop AG (Dortmund, Germany)                 | <i>Halomonas elongata</i>                | Halophilic bacteria             |
| Exopolysaccharides (EPS)            | Abyssine®               | Lucas Meyer Cosmet-ics (Québec, QC, Canada)  | <i>Alteromonas macleodii</i>             | Piezophilic (deep-sea bacteria) |

### 6.1. Superoxide Dismutases (SODs)

Superoxide dismutases are antioxidant enzymes found in most living systems, which are involved in the breakdown of superoxide radicals into hydrogen peroxide and molecular oxygen. The hydrogen peroxide is later converted into water and oxygen by enzymes such as peroxidases and catalases [144,145]. SODs with high catalytic functions have been identified in extremophilic organisms, and given their stability under varying conditions, they are an excellent source of biocatalysts for industrial applications [145]. A review of SOD, its different forms, such as Cu-Zn SOD, FE-SOD, Mn-SOD, and Ni-SOD, has been carried out [144].

SODs have potential applications in the medical industry as they can reduce and/or prevent oxidative stress associated with a variety of illnesses such as cardiovascular diseases, cancer, diabetes, infertility, neurological disorders, rheumatoid arthritis, and asthma. Their stability at high temperatures (up to 80 °C) and extreme pHs makes them excellent candidates for potential therapeutic applications for these different diseases [2]. These SODs can potentially be incorporated or engineered into different pharmaceutical products (e.g., antioxidant creams and medications) to provide robust antioxidant protection. For example, Mn-SOD from thermoacidophilic *Alicyclobacillus* (Firmicutes), which is stable at temperatures up to 80 °C and a pH range of 2–10 (stable in acidic stomach-like environment), has been touted as a candidate for use in medical applications and as a food additive because of its inherent robustness [127].

They can also be used in cosmetics and skin care products as biosensors and for product preservation. For example, SODs from the thermo-halophilic *Aeropyrum pernix* (Thermoproteota) (SODAp) and the thermo-acidophilic *Saccharolobus solfataricus* (Thermoproteota) (SODSs) heterologously expressed in transgenic tomato cell cultures using

recombinant DNA technology were stable at high salt, low pH, and high temperatures. Therefore, they can be used as natural additives for food preservation or as dietary supplements [145]. Extracted SODs from thermophilic organisms *Oceanobacillus saliphilus* (Firmicutes) and *Geobacillus thermoleovorans* (Firmicutes) were found to show significant resistance to heat and extreme pH conditions, compared to traditional mesophilic SODs, indicating that they will be excellent candidates for use in cosmetic, medical, and industrial applications [2].

Some current commercial uses of SOD are briefly discussed. The review by [96] identified SODs from extremophiles, or those engineered to be stable at high temperatures. These include Biocell™ SOD (from Lonza (Singapore), stable at 45 °C, used in skin and hair care products) and Native *Geobacillus stearothermophilus* (firmicutes) SOD (from Creative Enzymes (Shirley, NY, USA), active at 60 °C, with medical, cosmetic, and nutritional applications). However, despite their enormous potential, evidence of their use is limited because significant challenges remain in translating this potential into medical products with reliable delivery systems and sustained product efficiency to achieve desired product outcomes.

### 6.2. Catalases

Catalases from extremophilic organisms can potentially be used in different industries, including those involved in biomedical, food, manufacturing (e.g., the textile industry), and environmental bioremediation [146,147]. They are used as biocatalysts due to their stability and robust performance under extreme conditions [96,148]. This gives them a competitive advantage over catalases from mesophilic systems, which may struggle to function optimally under extremes of environmental conditions (such as extreme temperatures, pH levels, and salinity) and stressful industrial conditions [148].

Catalases from extremophilic and non-extremophilic sources can be used to remove hydrogen peroxide from fabrics in the textile industry [149]. Current applications of such catalases for industrial use include the brand Oxy-Gone® T400 (active at 30–70 °C), manufactured by Genencor (Palo Alto, CA, USA), which is used to remove hydrogen peroxide from textiles before textile dye application [96]. Similarly, Conzyme® CAT50 (Sunsozymes, Beijing, China) and Terminox (Novozymes, Kalundborg, Denmark), both active at up to 50 °C, are used to remove residual hydrogen peroxide after textile bleaching as part of post-bleaching clean-up processes before other downstream processes [96].

These catalases are also used in hydrogen peroxide removal in the food industry, for research, diagnostics, and wastewater treatment [150]. For example, Swissaustal commercially produces and sells thermostable catalase in both liquid and powder forms for research and industrial applications (<https://www.swissaustal.com/shop/category/1>, accessed on 18 February 2026). Another company, Creative Enzymes, sells a thermostable fungal catalase used to remove hydrogen peroxide in the textile industry, semiconductor, and HPPO factories. The enzyme is stable at 70 °C ([https://www.creative-enzymes.com/product/native-thermostable-fungi-catalase-for-semiconductor-process\\_16150.html](https://www.creative-enzymes.com/product/native-thermostable-fungi-catalase-for-semiconductor-process_16150.html), accessed on 18 February 2026). While catalases from non-extremophiles can be used in skincare products to neutralise free radicals and protect skin from UV radiation [151], no information on the commercial application for these enzymes from extremophiles was available.

### 6.3. Carotenoids

The carotenoids market is growing and is estimated to reach USD 2.0 billion by the year 2026, with the most valuable examples of marketed carotenoids including astaxanthin, canthaxanthin,  $\beta$ -carotene, lutein, and lycopene [152]. They have widespread application

in the cosmetic industry, the aquaculture industry, animal husbandry, and in the food industry as food colourants, food and feed additives, and supplements [153]. In the medical industry, reviews of the literature have shown that these carotenoids are anti-inflammatory, anticancer, improve cardiovascular health (astaxanthin, lutein, and lycopene), prevent liver fibrosis, and prevent night blindness ( $\beta$ -carotene) [152]. A review of the therapeutic uses of natural astaxanthin based on evidence from human clinical trials has been carried out [37].

Microalgae are excellent feedstock for high-value compounds. For example, *H. lacustris* (*pluvialis*) is one of the most commercially important microalgae because it is the primary source of the carotenoid, astaxanthin, which is considered to be a “super antioxidant” because of its high potency, as its antioxidant activities are ten times higher than those observed in lutein or  $\beta$ -carotene [18,154]. *H. lacustris* (*pluvialis*) is known to naturally produce the highest concentration of astaxanthin (5% of antioxidants on a dry weight basis) under stressful conditions [18,19]. It is a high-value microalgal product that has already been commercialised as a nutritional and health supplement in foods and in animal feeds. Cryophilic microalga *C. nivalis* is also known to produce significant levels of astaxanthin [19].

Astaxanthin from *H. lacustris* (*pluvialis*) has been marketed in various formulations for food use as dietary supplements after regulatory approval in countries such as the US and UK. Major producers include DSM (Maastricht, The Netherlands), BASF (Levallois-Perret, France), NHU (Shaoxing, China), Cyanotech (Kailua-Kona, HI, USA), AstaReal (Nacka, Sweden), and Algatech (Harrison, NY, USA) [155,156]. Astaxanthin-based products are available in different forms: syrups, tablets, soft gels, granulated powders, oils, and creams. Other forms of regulatory approval have been secured in multiple jurisdictions: *H. lacustris* (*pluvialis*) CO<sub>2</sub>-based extracts were granted a “novel food” status by the UK Food Standards Agency (FSA). In contrast, astaxanthin from *H. lacustris* (*pluvialis*) was given “GRAS” status (Generally Recognised As Safe) by the US FDA (Food and Drug Administration) [157,158].

$\beta$ -carotene is commercially produced from *Dunaliella salina*, which can tolerate highly saline conditions exceeding 300 g/L [18]. The latter *Dunaliella salina* can accumulate up to 14%  $\beta$ -carotene by dry weight, far more than any synthetic variants in antioxidant activity [19,159]. Canthaxanthin is a lipid-soluble antioxidant derived from the halophilic archaeon *Haloferax alexandrine* (Euryarchaeota). It is used as a feed additive in agriculture, in poultry, fish, and crustacean farms, and is also used in the cosmetic industry as the key ingredient in tanning pills [160,161]. Detailed reviews of the sources and the commercial applications of other carotenoids, such as canthaxanthin and lutein (xanthophylls), have been carried out [19]. In contrast, carotenoids from extremophilic microbial groups such as *Halococcus morrhuae* (archaea) and *Thermus filiformis* (bacteria), despite their potent antioxidant properties, are yet to be successfully commercialised. Deinoxanthin (DXT), a C40 monocyclic carotenoid produced by the extremophilic *Deinococcus radiodurans*, which is a promising food-grade antioxidant pigment and a potential anti-tumour agent, has yet to find a commercial application [20,103].

## 7. Conclusions

This review highlights the potentially substantial functional advantages of extremophilic antioxidants compared with those from conventional sources. Their intrinsic stability under extreme conditions, including temperature, salinity, and pH, makes them excellent candidates for biotechnological, industrial, and biomedical applications. Using specific examples such as superoxide dismutase, catalase, carotenoids, melanin, and peroxidases, their outstanding abilities to survive and maintain high operational efficiency under harsh, stressful conditions that would inactivate conventional enzymes are discussed. These underscore their potential for use in medicine (pharmaceuticals), food (nutritional

supplementation and preservation), agriculture, cosmetics, and other industries. Overall, extremophile-derived antioxidants are an emerging, stable, and potent resource for combating oxidative stress and for nutritional supplementation to improve health outcomes, enhance product stability and preservation, and support research and sustainable bioprocessing. However, challenges remain in developing cost-effective production and delivery systems that are not adversely affected in functionality, highly scalable, and capable of overcoming regulatory hurdles.

Future research should focus on obtaining more extremophilic microorganisms from other extreme environments, such as caves, and on expanding genomic and molecular exploration of understudied extremophiles to identify novel antioxidant enzymes with desirable properties. For most extremozymes, gaps currently exist between laboratory-validated stability and functionality and their real-life applications, underscoring the need for large-scale bioprocess optimisation, bioreactor design, and downstream purification. This is critical to making their commercial production economically viable. Structural biology studies, molecular engineering, increased use of recombinant approaches for therapeutic and industrial applications, integration of artificial intelligence, multi-omics, machine learning, and synthetic biology will accelerate the discovery and development of new extremophilic antioxidants. This will position extremophilic antioxidants as next-generation tools for biotechnology and medicine.

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