Chapter

Haloarchaea May Contribute to the Colour of Avian Plumage in Marine Ecosystems

Rosa María Martínez-Espinosa and Javier Torregrosa-Crespo

Abstract

Some seabirds or coastal birds such as flamingos or pelicans display elegant pink or reddish colours. These colours are due to pigments that birds cannot synthesize de novo. Thus, this coloration is mainly originated from carotenoids ingested trough carotenoid rich food sources like microalgae (*Dunaliella*) or small shrimps (*Artemia*), which are microorganisms inhabiting the salty environments where the mentioned birds live. New advances in this field of knowledge have revealed that extreme microorganisms belonging to the haloarchaea group (Archaea Domain) may contribute significantly to the characteristic pink- red colour of flamingos' feathers for instance. Alive haloarchaea cells have been found on the surface of the feathers. Besides, the major carotenoid produced by haloarchaea (bacterioruberin) has also been identify within the feathers structure. This work summarizes the main contributions recently reported about this topic as well as general aspects regarding bacterioruberin as a powerful colour carotenoid. Discussions about potential role of these microorganisms in the life of seaside birds are also included.

Keywords: bacterioruberin, bird coloration, carotenoids, flamingos, natural pigments, plumage

1. Introduction

Coloration is one of the most conspicuous traits that varies among organisms. In the case of animals, colour is mainly due to: (i) the presence of pigments (carotenoids, melanin, turacoverdin, biliverdin, protoporphyrin, etc); (ii) light phenomena such as reflection/emission from animal structures (skin, feathers, etc.); (iii) the presence of microscopic structure in scales, bristles, or feathers, which give them brilliant iridescent colours (commonly named "structural colours") [1]; and (iv) general aspects related to genetics [2]. Due to these reasons, animals show different colours, which can slightly vary even between individuals belonging to the same species. Animal colorations are strongly linked to different biological roles: camouflage, sexual, social, and interspecific signalling, physical protection (against UV radiation for instance), and sexual dimorphism [3–6].

In the case of the birds, feathers play a key role in general coloration. Those that are red orange show these colours thanks to the presence of different carotenoids within their structures. Carotenoids are natural pigments widely spread in nature: chloroplasts and chromoplasts of plants, bacteria, archaea, microalgae, fungi and even phytoplankton [7–9]. All the mentioned organisms can synthesize carotenoids, but animals in general are not able to produce them *de novo* (aphids and spider mites are an exception, and it is assumed that they acquired this ability thanks to genes transferred from fungi [10]). Thus, animals obtain carotenoids from diet. After food uptake, they are mainly metabolized by the liver and intestinal epithelium [11] to be further incorporated into fatty tissues or other structures such as feathers, skin, eyes, etc.

There are over 600 known carotenoids classified into two classes: xanthophylls (which contain oxygen) and carotenes (which are hydrocarbons without oxygen). Thanks to their chemical structure, they absorb wavelengths ranging from 400–550 nanometres (violet to green light) [12]. Consequently, these pigments are deeply coloured yellow, orange or red. Some carotenoids have vitamin A activity (they can be converted into retinol) and most of them can also act as antioxidants. Recently, it has been stated that cytochrome P450 enzymes are also involved in red carotenoid coloration [13].

Red coloured birds inhabiting salted environments such as salt marshes, seaside ecosystems, salted lagoons etc. may often acquire carotenoids by ingesting small organisms or even microorganisms like yeast and algae. Thus, flamingos (*Phoenicopterus sp*.) filter-feed on brine shrimp (*Artemia salina*) and blue-green algae (*Dunaliella salina*) [14], which are high rich sources of carotenoids. They are broken down into pigments by liver enzymes and fully incorporated into tissues [15, 16].

The nature of the colour shown by red-pink feathers is one of the aspects strongly discussed during the last few years. Many works have demonstrated that the colour is due to the carotenoids obtained through the diet, whilst other studies suggested that other external factors like microorganisms or light phenomena could contribute to the final red-orange-pink phenotype. This chapter summarizes recent knowledge about the presence of alive microorganisms belonging to the Archaea domain on the surface of red-pink feathers thus may contributing to their colour. General aspects related to the carotenoids produced by haloarchaea inhabiting feathers of coastal birds are also discussed.

2. The colour of bird feathers

Bird feathers have been the aim of several works during the last two centuries. Thus, the first reports on bird plumage listed in databases like PUBMED, Web of Science or Scopus analysed aspects focused on the muscles in charge of the feathers movement [17] or their growth [18]. Other aspects of bird feathers related to biological roles like sexual selection, colonization strategies or signalling have also been extensively explored [19–23]. These aspects are intricately connected to the coloration of avian plumage.

The first detailed studies about the colour of bird feathers were published in indexed scientific journals in the middle fifties last century. Since then, around 500 manuscripts have been reported on this subject (**Figure 1**). It is worthy to note that the number of studies about the colouration of plumage significantly increased at the beginning of XXI century (**Figure 1**). However, the number of publications focused on the presence of carotenoids in bird feathers is lower compared to those related to other issues affecting the phenotype of birds (**Figure 1**). Bird coloration (mainly in feathers) is one of the most studied topics to elucidate the role of natural and sexual selection in the evolution of phenotypic diversity. Thus, the variety of vibrant plumage colours has evolved as a direct result of social and environmental pressures.

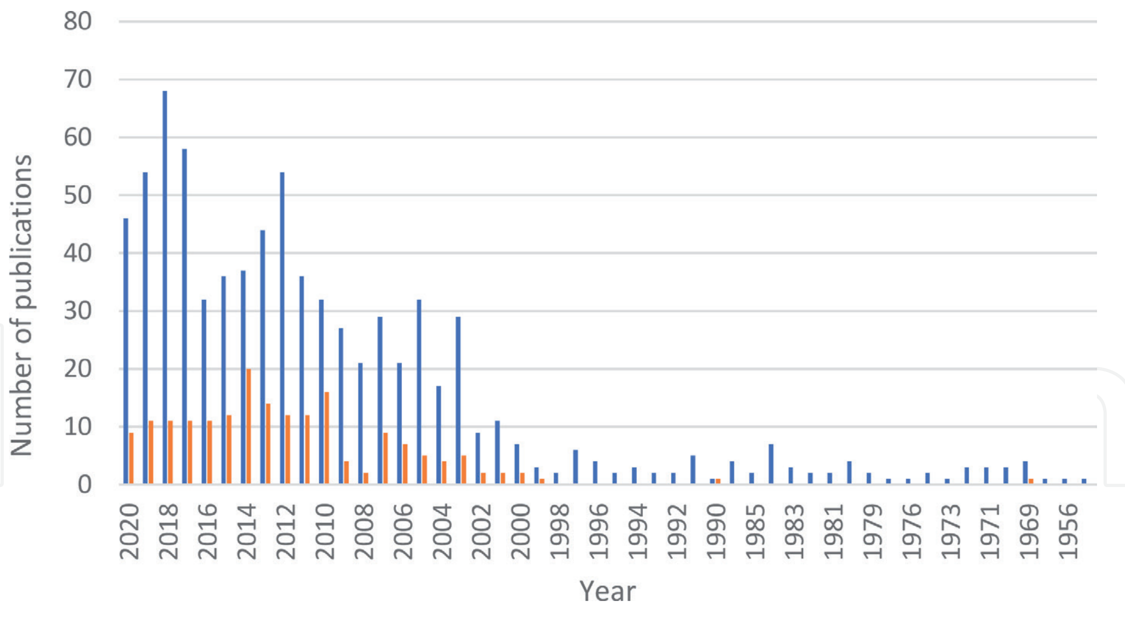

Figure 1.
Graph representation of the total number of publications per year from the database PubMed concerning the combination of the following keywords: (■) bird feathers AND colour; (■) bird feathers AND colour AND carotenoids. Revision date: 10th January 2021.

The colour of plumage and other structures in animals and plants is due to the presence of pigments (pigment-based coloration) or the presence of microscopically structured surfaces fine enough to interfere with visible light (structural coloration) [24]. Iridescence for instance, is one of the better-known examples of it [25]. In some cases, feather colours are the result of a combination of both [26, 27].

Table 1 summarizes the most representative pigments already identified as part of the colour of bird plumage. The most abundant are melanin and

Melanins		
Name	**Colour**	**References**
Eumelanin	Grey/Black	[28–31]
Pheomelanin	Brown	[28, 29, 31, 32]
Carotenoids		
Zeaxanthin	Yellow	[2, 33, 34]
Lutein	Bright Yellow	[2, 33–35]
β-carotene	Yellow	[2, 35]
β-cryptoxanthin	Yellow	[2, 35]
Canthaxanthin	Orange Red	[2, 33–35]
Astaxanthin	Red	[2, 34–36]
Rhodoxanthin	Purple-red	[34, 37, 38]
Porphyrins		
Turacoverdin	Green	[39]
Coproporphyrin III	Red Brown	[40]
Turacin	Red	[41]

Table 1.
Summary of the main features characterizing the most abundant pigments in bird feathers.

carotenoids [28, 42]. On the one hand, melanin-based coloration switches from brown to black due to the presence of phaeomelanin or eumelanin, respectively, or the number and distribution of the melanosomes [29, 30]. On the other hand, carotenoids-based colorations vary from yellow to red as previously mentioned.

The genetics of coloration in birds remains poorly described. However, it is extensively accepted that its expression is phenotypically plastic with a high sensitivity to variation in environmental conditions. Therefore, the melanin-based colour should be considered the key system to understand the molecular basis of phenotypic variations [43]. Some other pigments are only present in some species. This is the case of psittacofulvins, which are found just in a few species of parrots (*Psittacidae*) or penguins (*Spheniscidae*) [44–46] or turacoverdins, responsible for the bright green coloration of several birds of the family *Musophagidae*, most notably the turaco (*Turac*o sp.; *Musophagidae*). It is chemically related to turacin, a red pigment also found almost exclusively in turacos [39].

3. Haloarchaea

Archaea, one of the three Domains of life, make up a significant fraction of the microbial biomass on Earth [47]. It was thought that Archaea microbes were restricted to extreme environments, such as those with elevated temperatures, low or high pH, high salinity, or strict anoxia [48]. However, environmental sampling analysis based on rRNA sequences has revealed that archaea are widespread in "normal" ecosystems, including soils, oceans, marshlands, human colon, human oral cavity and even in human skin. They are particularly numerous in the oceans; thus, archaea in plankton may constitute one of the most abundant groups of organisms on the planet. From a metabolic point of view, they have evolved a variety of energy metabolisms using organic and/or inorganic electron donors and acceptors, playing important roles in the Earth's global geochemical cycles [49].

Salty environments are dominated by organisms commonly named "halophiles" (it comes from the Greek word for "salt-loving"). They are usually classified into three groups according to their NaCl requirements: slight halophiles (2–5% or 0.34–0.85 M), moderate halophiles (5–20% or 0.85–3.4 M) and extreme halophiles (20–30% or 3.4–5.1 M) [50].

Halophilic archaea, also called Haloarchaea, are extreme or moderated halophilic species inhabiting neutral saline environments such as salt lakes, marine salterns, marshes, saltern crystallizer ponds or genuine environments like the Dead Sea [51, 52]. In those natural ecosystems, salt concentrations are around 1.5–4 M, which corresponds to 9–30% of salts (w/v). NaCl is the predominant salt and ionic proportions are like those dissolved salts in seawater.

These halophilic ecosystems harbour a large diversity of microorganisms of all three domains: small eukaryotes such the shrimp *Artemia salina*, primary producers as the green algae *Dunaliell*a [14] (**Figure 2A** and **B**), aerobic heterotrophic bacteria (mainly belonging to the family *Halomonadaceae*), anaerobic fermentative bacteria (families *Halanaerobiaceae* and *Halobacteroidaceae*) and archaeal microorganisms of the families *Halobacteriaceae* and *Haloferacaceae* (commonly named "Haloarchaea"). They are mainly characterised by their red-orange-pink colour, which is due to the pigments they produce to be protected against the high sun radiation (**Figure 3**). Salted ponds for salt crystallisation or other salty ecosystems like de Dead Sea become completely red, mainly in summer, due to microbial blooms, in which haloarchaea of the genera *Haloarcula*, *Haloferax*, *Haloquadratu*m or bacterial species like *Salinibacter ruber* constitute de major populations (**Figures 2C** and **3**).

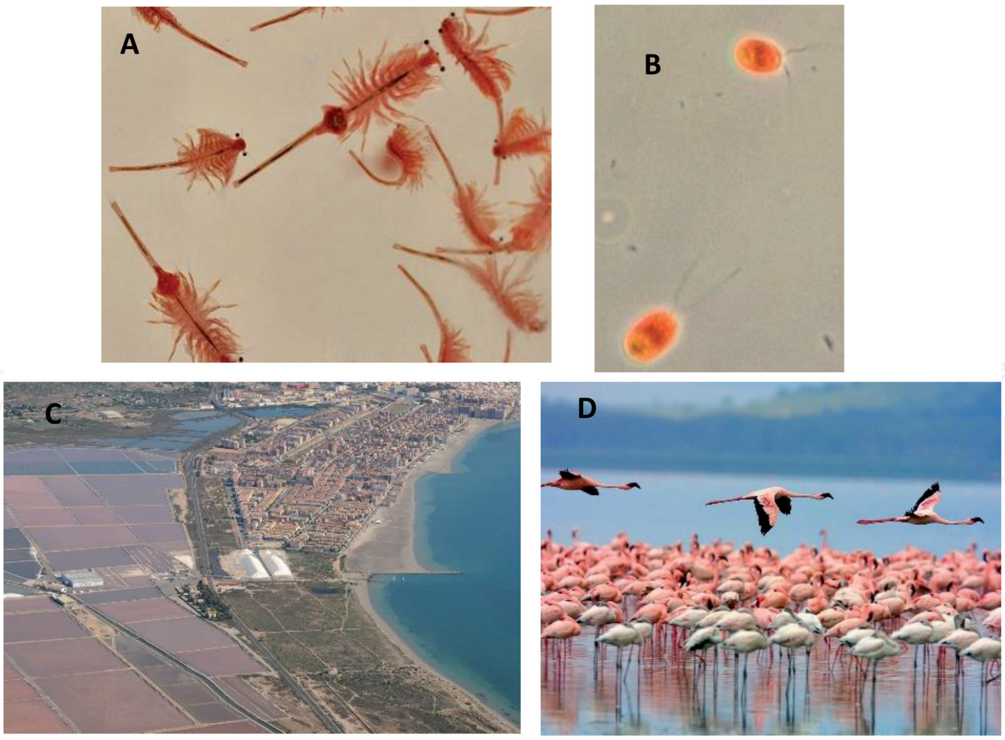

Figure 2.
(A) Artemia salina *and (B)* Dunaliella salina*. They constitute the major microbial populations in salted waters in coastal environments, salted lagoons, salty ponds from where NaCl is isolated from human consumption, etc. (C) Aerial overview of the saltern ponds located in Santa Pola city (Southeast of Spain) (http://paisajesturisticosvalencianos.com/paisajes/las-salinas-de-santa-pola-torrevieja/). This kind of ecosystems are warm places frequently inhabited by seaside birds like flamingos (D). The colour of the ponds is due to microbial blooms, which occur mainly in summer.*

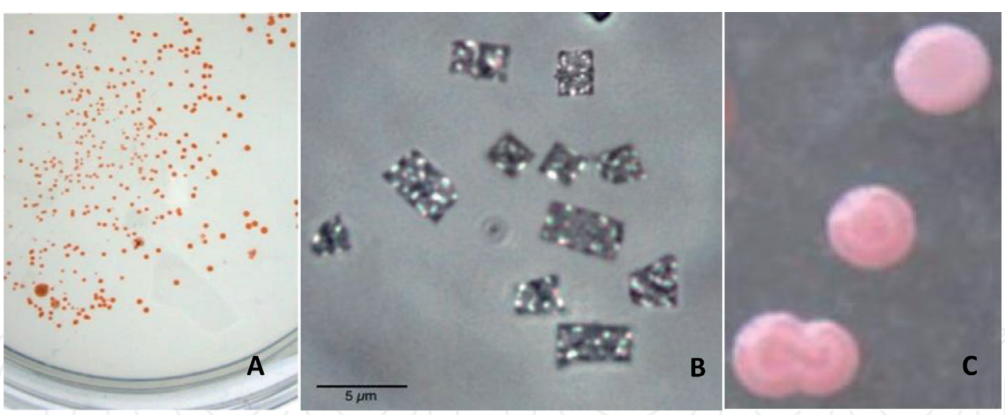

Figure 3.
(A) Haloferax volcanii *colonies; (B)* Haloquadratum walsbii *cells (picture from https://microbewiki.kenyon.edu/index.php/Haloquadra) and (C)* Haloferax mediterranei *colonies. Flamingos display haloarchaeal colours, they often frequent hypersaline lakes, and they carry haloarchaea with them on their travels around the world.*

4. Haloarchaea and their relation to avian plumage colour: the case of marine birds

Studies in the early nineties of the last century demonstrated that the carotenoids of the feathers were derived from the diet and deposited within tissues selectively [53] being the liver one of the most important organs involved in the conversion of carotenoids uptaken [54]. Some years before, other studies focused on seaside birds as flamingos stated that the major carotenoids in blood and feathers were canthaxanthin and a rare β-carotene derivative (4-keto-α-carotene) [55, 56]. Limitations on chemical and analytical techniques have contribute to the poor knowledge about carotenoids in birds up to nowadays. Fortunately, new advances in spectrometry and HPLC have made possible a significant improvement in this field of knowledge [41, 57]. Thus, during the last 15 years, several research groups worldwide have characterised the nature (and even the concentrations) of carotenoids in blood and feathers, mainly in finches [58, 59] and parrots [44, 60]. All the reported results show that the most important carotenoids contributing to the red-orange-pink colours in feathers are: canthaxanthin, astaxanthin, zeaxanthin and carotene (including its derivatives). In the case of seaside birds, it has been stated that the main rich carotenoids sources are the small shrimps and algae co-inhabiting the salty environments (*Artemia* and *Dunaliella* species, for instance) (**Figure 2**). Consequently, it is extensively assumed that the major pigments in marine bird's feathers would be those predominating in shrimps and algae (astaxanthin, canthaxanthin and carotene). However, some other studies indicate that in hypersaline habitats the birds do not feed extensively on brine shrimps *Artemia* to avoid salt stress [61]. Therefore, other carotenoid rich sources must be considered as part of the diet of marine birds to explain their pigmentation.

Recent contributions in this field have revealed that there are other important factors contributing to the red-orange-pink colour of the feathers. Between them, it is important to highlight the following: (i) genetics [2]; (ii) variation in carotenoid-protein interactions in bird feathers structures, which produces novel plumage coloration [62] and (iii) the presence of alive red-orange microorganisms on the surface of the feathers [63]. This last factor has recently been reported from flamingos growing up in captivity: viable, red-coloured archaeal strains belonging to the genera *Halococcus* and *Halogeometricum* were isolated from the surface of the plumage [63]. Apart from these viable cells, metagenomics approaches showed that cells belonging to other genera such as *Haloquadratum*, *Haloferax*, *Haloarcula*, *Halorubrum* and *Natronomonas* are also present on the surface of the flamingos' feathers. This kind of haloarchaea can produce significant amounts of bacterioruberin, a carotenoid mainly synthesised by them giving the microbial cells red-orange colours [8, 64, 65]. Besides, the analysis of the flamingo plumage pigments shows that bacterioruberin is not only in the alive microbial cells on the feathers' surface, but also found inside the flamingo feathers structure. This result directly suggests that haloarchaea are also part of the diet of flamingos. Bacterioruberin is responsible for the colour of these extremophilic microorganisms (**Figures 3** and **4**) [8, 65]. It has a primary conjugated isoprenoid chain length of 13 C=C units with no subsidiary conjugation arising from terminal groups, which contain four –OH group functionalities only (**Figure 4**).

This carotenoid is involved in several biological roles in haloarchaea: it protects the cells against the damage produced by high intensities of sun radiation, it provides aid in photoreactivation [66] and it promotes membranes stability [8, 65]. Characterisation of pure bacterioruberin samples revealed that it is more powerful than carotene as antioxidant compound [67, 68]. Due to these facts, bacterioruberin could be used in biotechnology and biomedicine for different purposes [8, 69].

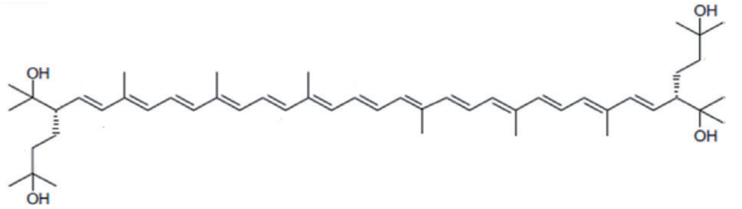

Figure 4.
Chemical structure of bacterioruberin. This compound has promising potential uses as antioxidant, antitumoral and immunomodulatory molecule for pharmaceutical and cosmetical formulations [64, 65].

Consequently, haloarchaea in general and their pigments in particular, may contribute to the orange-red colour of the feathers in two ways: (i) pink-red haloarchaea cells on the surface contribute to the pink-red phenotype in flamingos' feathers and (ii) haloarchaeal cells are part of the marine birds' diet (at least flamingos), consequently their carotenoids (mainly bacterioruberin) are ingested, metabolised and further assimilated.

5. Conclusions

New advances in the knowledge of animal pigmentation state that not only the pigments (carotenoids, melanin, etc.), but also the microstructure of the feathers as well as external factors, contribute to the final phenotype in terms of coloration. Related to birds, and particularly to seaside birds, it was thought that microalgae and small shrimps were the major sources of carotenoids so far. Nevertheless, recent results revealed that other small microbes such as haloarchaea could contribute significantly to the red-orange colours showed by birds like flamingos. In that sense, bacterioruberin becomes a new pigment to be considered to explain animal colours in marine environments. The potential influence of haloarchaea as an environmental factor determining avian plumage coloration or even protecting the microstructures of feathers against UV radiation must be investigated in further studies. Although bacterioruberin has been very well described, only few studies about its biological implications are available at the time of writing this review. Thus, more efforts must be done to explain basic aspects related to bacterioruberin metabolism and its effects on animal health and animal phenotypes. On the other hand, associations between different haloarchaeal-bird species as well as changes in these associations promoted by environmental conditions or anthropogenic actions are worthy to be analysed into detail. Hypothesis based on potential symbiotic relationship between haloarchaea and seaside birds remains unexplored.

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Conflict of interest

The authors declare no conflict of interest.

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