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REVIEW

# Diversity of Pigments in Insects, Their Synthesis and Economic Value for Various Industries

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ABSTRACT

Pigments play an essential role in imparting colors to the various organs of invertebrates particularly, insects. Genetic evolution and adaptive pigmentation of invertebrates have been studied which depicted that insect colors respond to the climatic changes. The physical, chemical and structural properties of insect pigments are being studied by researchers for years to elucidate their evolutionary aspects of physiology, metabolism, and economic importance for human welfare. Color development in insects varies within the species of different genera. In this state-of-the-art literature review, we discuss the variety of pigments other than visual ones found in different species of insects. The review also highlights the potential benefits or functions of pigments to insects.

## 1. Introduction

There exists a large variety of colorful insects around us. Such insects attract our attention wherever we go. However, it is fascinating to understand the evolution of these colors within the bodies of insects. Any substance which changes the color of transmitted or reflected light when falls on it due to the result of wavelength of selective absorption is called a pigment. These pigments are responsible for imparting different colors that we see around us. Natural pigmentation is used in various species of animals including insects for different life strategies such as aposematism (warning), camouflage, mimicry, sexual selection, and other forms of signaling [1]. Apart from visual pigments, there exist a variety of pigments produced by different insects that are involved in the growth, metamorphosis, and other developmental stages of an insect's life [2]. The aesthetic value of insects is enhanced by their attractive colors which have proved useful for them by protecting against pests and predators. Colors not only add beauty to insects but their brightness gives warning signals to the enemies to keep away from them. Various insect pigments along with the economically important color pigments found in many insect species have been reviewed here.

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## 2. Pigment Patterns and Synthesis

In insects, pigmentation is the process of the development of different colors, occurring in a variety of patterns during the developmental phenomenon. Mostly, color development occurs in the adult stage of the insects [3]. This not only involves pigment patterning and synthesis, but many aspects of this process significantly influence phenotypes and behavioral aspects of insects in one or the other way [4]. The pigmentation in insects is achieved by exploiting different pathways. Some pigments can be synthesized by cyclization of linear precursors, viz., anthraquinone, aphin, and tetrapyrroles, those derived from cyclic precursors such as pterin, ommochromes, melanin, and anthocyanin [5]. Apart from providing body coloration, some pigments are pivotal for the balanced physiology of insects, e.g., melanin protects the body against harmful ultraviolet (UV) radiations. Some ommochromes act as visual pigments, while tetrapyrroles facilitate oxygen transport to cells of the body.

The ease of artificially rearing fruit fly, *Drosophila melanogaster* in laboratory serves as a pivotal model to study physiology related to pigmentation in insects [6]. The process of pigmentation occurs in two stages, namely, localization of pigmentation in the body followed by biochemical synthesis. These phenomena are chiefly regulated by patterning genes and effector genes. Whereby the patterning genes manage the distribution of pigment cells by directly or indirectly activating the expression of effector genes that transcribe enzymes and other co-factors involved in the pigment biosynthesis. For instance, wing pigmentation in butterflies such as *Heliconius* sp. patterning genes similar to those in *Drosophila* have been discovered. Different developmental stages show various patterns either through mutation or in response to external conditions such as weather, temperature, and moisture. Many genetic loci in *Heliconius* butterflies are shown to be involved in the color pattern of wings of this species [2]. Once patterning genes determine the location of pigmentation, thereafter the effector genes initiate to encode the enzymes for pigment production. Thus, effector genes determine the nature and quantity of pigments produced [4].

## 3. Evolution, Genetics, and Pigmentation

The study of pigmentation is pivotal to conjecture the evolution, genetics, and developmental biology of the insect. The pigmentation system of insects elucidates the nature of adaptations by linking genetic traits to variation in body fitness [7]. Mutations that affect the synthesis of brown eye pigment, Xanthommatin, have been investigated in combination with chocolate and red cells. These mutations cause ectopic pigmentation of the malpighian tubules as well as fat body of larvae, which synthesizes pigment precursors. Mason and Mason recently reviewed the comparative biology involved in the pigmentation in insects [8]. Moreover, the results of molecular studies for pigment transcribing genes in lower vertebrates were compared with similar data from mice and man, to emphasize the developmental and evolutionary perspectives of pigmentation. These advanced studies related to pigmentation of lower vertebrates allowed the comparison of orthologous molecules across a broad range of species. Moreover, these studies addressed the evolutionary questions to highlight the differences and similarities in pigmentation between mammals or birds and other vertebrates. Thus, developmental and evolutionary data can be useful to create a unified view of pigment cells and pigments across many species [8].

Briscoe and colleagues have studied the physiological, molecular, and neural mechanisms of insect color vision [9]. Though the lifestyles of many insects differ from each other they possess identical color receptors. They proposed that chance evolutionary processes, history, and constraints are the factors that are more influential, instead of mere adaptations. Analysis based on phylogeny to explore such factors suggested that variation between individuals and populations and quantitation of fitness of the adaptive value of characters helps to identify insect color vision systems [9]. Brakefield and French discussed the concentric eyespot patterns on wings of butterflies which are formed by seasonal polyphenism [10]. Moreover, the evolutionary aspects of color vision of insects concerning ecological factors have been reviewed recently.

## 4. Role of Color in Insects

Insects have various body colors that perform a tremendous array of functions thus augment the insect for adaptation. Badejo and coworkers reviewed few social insects, namely, ants, wasps, and bees for the usefulness of their body colors. Colors play a role in signaling for wasps and act as sources for finding newer ecological indicators and biomarkers. It has been stated that red and brown ants use color for camouflage while black ants use melanin for thermoregulation and protection from pathogens. Similarly, pigmentation helps the wasps and bees to adapt to the thermal conditions existent in the surrounding environments [11].

Insausti and coworkers studied the role of pigments in the photodamage and oxidative stress of insect eyes [12]. Similarly, Stavenga carried out pioneering studies on insect retinal pigments [13]. However, the elaboration of visual pigments is beyond the scope of this review. Carotenoids

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are ubiquitous organic compounds that are involved in the important functions across all organisms. Additionally, Heath and colleagues reviewed the importance of carotenoids in insects and how these carotenoids and their derivatives influence interactions between insects and plants [14]. They also reviewed the structure and biosynthesis of these molecules and their importance in vision, photoperiodism, diapause, and their potential antioxidant role in signaling. Further, they investigated the functions of carotenoid derivatives like strigolactones and apo-carotenoids during the plant-pest and insect- parasitoid interactions [14].

In insects such as *Menduca sexta*, the color of hemolymph is green due to the green leaves ingested by them as natural food, however when fed on an artificial diet the color changes to blue, thereby elucidating the impact of the diet on insect's physiology. The green pigmentation is a result of two chemicals, such as Biliverdin, (blue pigment) and lutein, which is a yellow pigment. Since the artificial diet contains little amount of lutein and *Manduca* spp. lacks genes responsible for lutein synthesis thus they appear blue than their counterparts which feed on green plants. In *Manduca* sexta, the chemical compound lutein is the only carotenoid that is absorbed through the gut. This process is largely possible due to the presence of lutein-specific transporters present in the gut-systems.

## 5. Respiratory Pigments

The watery fluid hemolymph is the blood of insects that fills the hemocoel of the body. It is known to contain many ions, along with a variety of molecules and cell types. Hemolymph is usually clear and colorless in the majority of insects; however, few species contain different pigments, imparting a green, yellow, and blue color. Similarly, some rare cases do exist where the hemolymph is red due to the presence of hemoglobin such as immature aquatic and endo-parasitic flies. Green pigments of the hemolymph of insects are known to circulate completely within the insect body. Like human blood, bug blood carries nutrients and hormones to the cells of insect organs. The greenish or yellowish color of insect blood comes from the plant pigments being consumed by the pest [15]. Insects display green colors because of "porphyrin" pigments, due to the green leaves of plants on which they feed. This imparts green color to the feces of the insect as well.

## 6. Diversity of Pigments in Insects

A variety of pigments are found in insects, each with unique functions for the benefit of the organism that possesses it (Table 1). Some of the most commonly observed and useful pigments of insects are discussed below.

**Table 1.** A list of different pigments and their respective functions observed in insects.

| Organ type | Pigment | Colour | Function | Example |
|---|---|---|---|---|
| Respiratory | Bilin | green, blue yellow | Haemolymph | Green Huntsman Spider |
| | Chlorocruorin (Mesobiliverdin) | green | | Pieris rapae, Ezara viridula |
| | Haemocyanin | blue | Blood | Spider |
| | Haemoerythrin | red | | *Sipunculid* spp. |
| Cuticle | Biliverdin and lutein Melanin Indole Catechole | green/ black | Tissue fluid Skin | *Menduca sexta* *Drosophila* spp. |
| Fat body | Bilin | white, yellow, tan, and brown to blue | Adipocytes, trophocytes, Oenocytes | Mosquito |

In Odonata insects, the molecular mechanisms of pigment formation, especially, with reference to the light blue coloration of epidermis has been extensively studied. It has been observed that genes involved in biosynthesis of three major insect pigments are conserved across insect groups [16]. In Odonata the ommochrome pigments develop on the proximal layer while pteridines appear on the distal layer of epidermis. These pigments impart light blue color to the insect body. In dragonflies and damselflies, two ommochrome pigments, viz., Xanthommatin and decarboxylated Xanthommatin are pivotal for the body coloration of male individuals. The redox reactions of these pigments transform the male individuals from yellow to red during maturation from nymphal stages [17]. Similarly, pteridine pigments are found on many body regions of the dragonflies where they emit fluorescence under UV radiation [16].

### 6.1 Chlorocruorin

Chlorocruorin (Greek *khlōros* means green and Latin *cruor* meaning blood) is a greenish heme-containing respiratory pigment. It exists in the blood plasma of polychaete worms. Likewise, in insects such as *Menduca sexta*, the colour of hemolymph is green due to the presence of Chlorocruorin. Though, it closely resembles with hemoglobin but its affinity for oxygen is comparatively very low. The greenish hemolymph of butterflies, *Pieris rapae*, *Amphipyra sanguinipuncta* and *Cacoecia australana*, is due to β-carotene and lutein while the blue component is probably due to mesobiliverdin which is a tetrapyrrolic bile pigment. In Pentatomid bug, *Nezara viridula* the green hemolymph contains β-carotene proteins complexed with blue pigment which is similar to anthocyanin. The



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physiology and origin of these pigments were discussed earlier by Hackman [18].

Onelli and others studied the exoskeleton colour development of dock leaf beetle, *Gastrophysa viridula* [19]. They showed the structural coloration by electron and light microscopy of the cuticle formation during the developmental stages of egg to adult stage of *Gastrophysa viridula*. Developmental stages show the colour transformation from yellow (egg), orange (larva & pupa), orange mixed with green (emerged imago five days after ecdysis) and green (final cuticle formation).

## 6.2 Haemocyanin

Insects are deficient of blood vessels instead they possess hollow space below their external skeleton where the hemolymph circulates. The pumping of the haemolymph is a relatively slow process which tentatively takes about eight minutes for complete circulation of the blood. In spiders the exchange of gases such as oxygen and carbon dioxide is carried out by a respiratory pigment protein, called hemocyanin. Haemocyanin is the respiratory protein that transports oxygen in the invertebrates like insects. It is generally observed in the blood of arthropods such as crabs, and lobsters apart from some molluscs. A hemocyanin molecule contains two atoms of copper that bind with oxygen. Due to the binding of the $O_2$ the copper atom changes the colourless deoxygenated form 'Cu I' into the blue oxygenated form 'Cu II'. In some animals, haemocyanin forms giant polymers of large molecular weights. Unlike hemoglobin, hemocyanin does not binds to the blood cells. Moreover, hemocyanin is not much efficient in binding to gases. Thus it is found in very few species of insects and spiders. Instead, insects have evolved with a tracheal system to directly mediate the transfer of oxygen to the tissues through trachea.

## 6.3 Fat Body Pigments

Fat body in insects is known to play a vital role in the storage and transport of hemolymph compounds. Among the different hemocytes, adipocytes (trophocytes) are the predominant cells associated with vital metabolic and storage functions. The color of adipocytes, depends on the insect species and changes with maturation. The fat body of mosquitoes made from cell masses of trophocytes and oenocytes contains lobes that project into the hemocoel. The trophocytes contain a high amount of lipid droplets and protein granules. Martins and coworkers compared the overall structure of the fat bodies of five mosquito species where brown pigment granules were localized exclusively in the trophocytes of thorax and dorsal integument [20]. Th brown pigmented trophocytes were observed only in case of *Anopheles aquasalis* and *Anopheles darlingi* but not in *Aedes* spp. This suggests that these cells play a role in detoxification via ommochrome storage. A comparative analysis of the fat body in five different mosquito species shows a significant contribution towards understanding of the structural-function relationships associated with this organ [21].

## 6.4 Melanin

Melanin is the broad term for a group of natural, dark pigments which occur in animals and plants. They are usually bound to protein. Melanins are grouped as "indole" or "catechol", depending upon the reaction products formed on alkali fusion and permanganate oxidation. However, most of the melanins examined from animal sources so far are of the indole type, (Figure 1) where they are formed from the oxidation of tyrosine and dopamine (DOPA). The process of melanin secretion is a multistage process called melanogenesis where tyrosine is oxidized and then a polymerization reaction follows. Melanins are synthesized by specialized cells called melanocytes. Melanin has 5 basic variants such as allomelanin, eumelanin, neuromelanin, pheomelanin, and pyomelanin [22]. The melanins of mammals and cephalopods have been studied extensively while in some cases the chemical composition and reaction mechanism are also investigated (Figure 2). The enzyme involved in the melanin synthesis is a phenolase which acts on phenolic substrates. However, their complete structure is not known yet. Melanins that are derived from tyrosine, are usually formed from indolyl units [23]. In arthropods, melanin is deposited in layers to create Braggs reflector, of alternate refractive index. In insects when the pattern of scales matches, it gives a characteristic and iridescent coloration to different species.

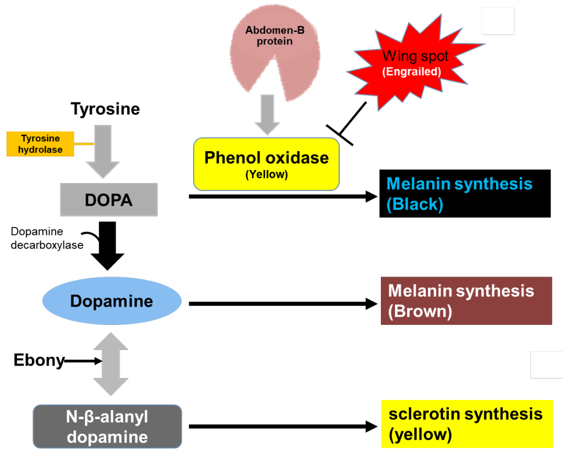


**Figure 1.** Schematic representation of melanin synthesis in *Drosophila melanogaster*. Modified from Wittkopp and Beldade [4].

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The process of pigmentation occurs in two stages, namely, localization of pigmentation in the body followed by biochemical synthesis. These phenomena are chiefly regulated by patterning genes and effector gene, where the patterning genes manage distribution of pigment cells by directly or indirectly activating the expression of effector genes. The effector genes transcribe enzymes and other co-factors involved in the pigment biosynthesis. For instance, during wing pigmentation in butterfly, *Heliconius* spp., the patterning genes similar to those in *Drosophila* spp. have been discovered. Different developmental stages show various patterns either through mutation or in response to the external conditions such as, weather, temperature and moisture. Many genetic loci in *Heliconius* spp. butterflies are shown to be involved in color pattern of wings of this species [2]. The patterning genes determine location of pigmentation and, thereafter the effector genes initiate to encode the enzymes for pigment production. Thus, effector genes determine the nature and quantity of pigments produced [4].

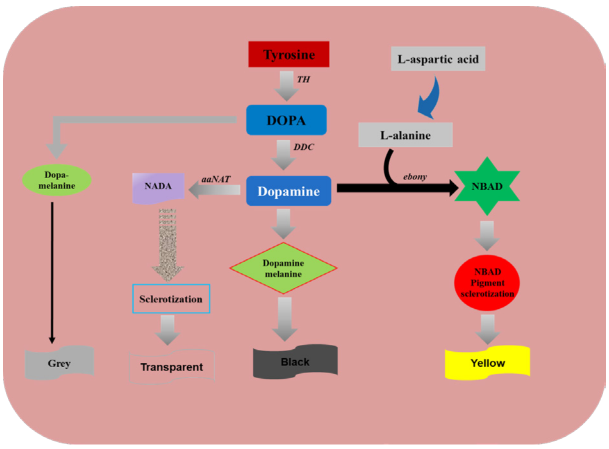


**Figure 2.** Schematic overview of the melanin pathways involved in pigment production of insects. (modified from[4])

Fluorescence markers are responsible for transgenesis in most insects. Osanai-Futahashi with other colleagues established a transformation marker system which leads to phenotypes due to alterations in color of melanin pigments [24]. Their study showed that in silkworm, *Bombyx mori*, overexpression of aryl alkylamine-N-acetyl transferase changes the colour of newly hatched first-instar larvae from black to a distinctive light brown colour. Also, over expression in another gene, *B. mori* β-alanyl-dopamine synthetase (Bm-ebony) changes the larval body colour of older instars. The authors further demonstrated that ectopic Bm-arylalkylamine-N-acetyl transferase expression lightens coloration in ladybird beetle, *Harmonia axyridis* and fruit fly, *Drosophila melanogaster* [25].

## 7. Role of Pigmentation in the Polyphenism

Locust phase polyphenism is a phenomenon by which grasshoppers can form dense migrating swarms. Many studies have been carried out which helped to understand the causes of locust swarming. However, the evolutionary aspects of locust swarming that differentiates it from the non-swarming relatives are not established yet. Locusts are closely related to sedentary species that can express and display density dependent phenotypic plasticity. This in other words, explains the phylogenetic evolution of the swarming locusts which arises from a stepwise assemblage of conserved characters, that evolved during the diversification of grasshoppers. Carotenoids, bile pigments, melanin and ommochromes are responsible for coloration of locusts. Sometimes, Pteridines and flavonoids may also contribute [26] to some extent in the coloration of these insects. Tanaka and Paulpener investigated the neuroendocrine control of the dark body colour in hopper, *Locusta migratoria* using an albino strain as a bioassay system [27]. Methanol or saline extracts of corpora cardiaca of a normal, non-albino, strain was dried, dissolved in ethanol or mixed with peanut oil, and injected into albino hoppers. However, neither ethanol nor methanol extracts induce dark color whereas extract samples mixed with peanut oil induced dose-dependent darkening in the albino hoppers within a few days after injection. With increase in dose, the darkening of induced color increased.

The same researcher in 2006 summarized the phase polyphenism in locusts [28]. In, *Locusta migratoria* the injection of neuropeptide Corazonin induces different body colours in the albino nymphs which are generally observed solitary as well as gregarious locusts irrespective. Moreover, it has been stated that juvenile hormone and corazonin are both very important for the expression of green solitary forms normally found in the fields. Since corazonin and its similar chemicals are widespread in insects. Many researchers recently experimented that transplantation of corpora cardiaca to albino locusts indicated the presence and secretion of Corazonin in various insect species [28].

## 8. Commercial Value of Insect Pigments

It is well known that natural dyes obtained from plant sources are used to prepare various colour pigments, which are non-toxic. Like-wise from the dawn of the civilization, insect pigments have been used for the extraction of several dyes used in various industries. Here we provide a brief account of these dyes that have been obtained from insects and commercialized for various industries (Table 2).

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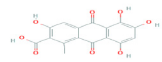
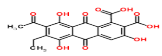
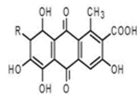
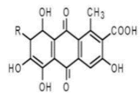
**Table 2.** Some of the insect pigments that are important for various industries.

| Pigment | Source | Structure | Colour | Applications |
|---|---|---|---|---|
| Kermesic Acid<br>Laccaic acid | *Kermes vermillio*, *Kermes palestinensis* | <br> | Orange red<br>Brilliant Red | Dye Industry |
| Cochineal | *Dactylopius coccus*, *Porphyrophora polonica* |  | Red | Medicine, Food production, Cosmetics & Fabric Dyeing |
| Carmine | Porphyrophora hamelii |  | Crimson<br>Brilliant red | Packaging labels in food and cosmetics, Hand-woven oriental rugs and royal outfits, food colorant, Painting works. |
| Lac & Shellac | *Kerria lacca*, *Laccifer lacca* | $C_{26}H_{35}N_3O_{11}$ | red from violet to brown | Varnishes, paints, Sealing wax, Coating of pills, Glossiness of fruits and vegetables, Confectionary food products. Vinyl records & Coloring military uniforms. |

### 8.1 Crimson Dyes

Scale insects have long been used to produce crimson dyes. The anthraquinone derivatives kermesic acid is orange-red in colour whereas, carminic acid, and laccaic acid are brilliant red in colour [29]. Kermesic acid is extracted from the shell of the female Kermes insects like (*Kermes vermillio, Kermes palestinensis*) which grow as immobile clusters on wood of trees. Kermes dye was later substituted by another rich dye called Cochineal [30].

### 8.2 Cochineal

The pigment cochineal is derived from scale insect, *Dactylopius coccus* which produces carminic acid to protect itself from insect predators. Cochineal dyes are non-toxic and non-carcinogenic and have applications in medicine, food and cosmetics. Cochineal is a stable dye and is most resistant natural colorant to excessive light, heat and oxidation as compared to synthetic colorants. Polish cochineal insects (*Porphyrophora polonica*) have commercial value as dyes for natural fabrics. It is derived from parasitic scale insects living on the roots of various herbs. The dye contains carminic acid and traces of kermesic acid.

### 8.3 Carmine Dye

Carmine is derived from carminic acid. The scale insects, such as Armenian cochineal *Porphyrophora hamelii* (Brandt) also known as Ararat cochineal or Ararat scale is the main producer of this pigment. It is deep crimson dye used to produce various shades of red, and frequently found in cosmetics as well as food coloring agents. Carmine dyes are used in packaging labels of food and cosmetics. It is much more concentrated than the traditional red dyes of madder root, kermes, polish cochineal. This insect dye has an important use in hand-woven oriental rugs and royal outfits. Carmine is also used to colour foods such as meat, bakery products and many cheese varieties and drinks such as juice and beverages. Due to being non-toxic to humans it is frequently applied in pharmaceutical products like ointments and pills. Carmine like pigment from scale insects such as brilliant red is used for painting purpose also.

### 8.4 Lac

Lac or shell lac is yet another useful product obtained from the strains of Lac insects such as *Kerria lacca, Paratachardina decolrella* and *Paratachardina pseudolobata*. The water-soluble red dye which comes mainly from body of Lac insect is obtained by aqueous extraction from 'stick lac' which is encrustation of insects surrounded by resin attached to the twig of the tree. Lac dye consists of laccaic acid or its analogs. The residue is further processed to produce seedlac and shellac. In India it is cultivated on three host plants namely, Kusum (*Schleichera oleosa*), Palas (*Butea monosperma*), and Ber (*Zizyphus mauritiana*). The two strains of the Lac insects, the Kusumi strain and the Rangeeni strain both produce deeper colored lac in natural and orchid plantation condition. Lac is used to dye natural fabrics such as wool and silk. The shades of red from violet to brown are used as mordants.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### 8.5 Shellac

It is a natural lacquer which is of the highest quality according to its clarity. Both seed lac and shellac are used in applications including varnishes, paints, sealing wax, coating of pills and to increase glossiness of fruits and vegetables and confectionary products. Shellac is importantly used in making vinyl records and to colour the uniforms of Indian military. Shellac is available in shades from yellow to deep orange, and may be bleached white for use as carpet dyes. Processed seedlac and shellac contain lower amounts of laccaic acids, however, rich in water insoluble yellow pigment 'erythrolaccin', is concentrated in the excreted resin [31].

## 9. Summary and Future Prospects

Here we review the pigmentation of insects and their potential economic value. Insects as minute creatures possess unique features which augment them to adapt to the surrounding environments and different pigments impart beautiful colours to their bodily appearance. The role of colour in many insect species has been studied in the past from the point of view of nature as well as genetic evolution of insects. Induced and spontaneous mutations have been investigated in various insect species as well. Usefulness of genetic markers for transgenesis studies in diverse insect taxa has also been studied by various investigators earlier. The detailed mechanism, pattern and stages involved in the pigmentation during metamorphosis have been investigated in various species. This has been possible by discoveries of novel pathways with in-depth experiments carried out by entomologists, and insect physiologists around the world. However, the relationship of certain pigments with chromophores still awaits exploration. The function of insect pigments especially in pest insects and predators is an interesting area for further investigation that awaits exploration. The complexity of the color development, its relation to structural coloration and thermal regulation in insects is still elusive. This review also emphasized the industrial importance of insect pigments. The commercially important products derived from natural pigments of insects are being analyzed and applied for better prospects for human welfare. Their applications in other areas of industry as well as research can prove to be more user friendly in future. The desire for higher production of these pigments/dyes for industrial use also needs to speed up which is possible only through the genetic modification of the respective genes of insects. Also, the potential of colorful insects such as ants, beetles and grasshoppers as sources of proteins for animal feed and consumable protein food products by human beings needs to be explored further.

The attractiveness of butterflies is due to the distribution of their color pigments all over the body in various patterns where they serve many functions and purpose. These colors fascinate human eyes and so are being used as a tool to develop genetically modified new species of butterflies. This has led to the development of the concept of butterfly gardens all over the world for conservation of these insects. In the present era of advanced technology, an enormous number of new insect species are discovered all over the world. A detailed study of investigation of their pigments at the morphological, physiological, evolutionary and genetic levels will prove to be very useful as part of advanced entomological research. The use of the electroporation mediated RNAi technology to unravel the mechanism of color formation in insects is still at its nascent stage. Therefore, employment of the more advanced approaches is needed to understand the color formation patterns of insects. Moreover, the impact of climate change on color formation in insects has recently started to attract attention, however there is still a long way to extract standard conclusions for it.

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### Conflict of Interest

The authors declare that they have no conflict of interest with respect to the research, authorship, and/or publication of this article.

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