We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists

6,900

185,000

200M

Downloads

154
Countries delivered to

Our authors are among the

 $\mathsf{TOP}\:1\%$

most cited scientists

12.2%

Contributors from top 500 universities



WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index in Web of Science™ Core Collection (BKCI)

Interested in publishing with us? Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.

For more information visit www.intechopen.com





Diversity and Functions of Chromophores in Insects: A Review

Tanuja N. Bankar, Mudasir A. Dar and Radhakrishna S. Pandit

Additional information is available at the end of the chapter

http://dx.doi.org/10.5772/intechopen.74480

Abstract

Insects are the most diverse among the animal kingdom. The diversity of insects is ever increasing due to their fast adaptability to the rapidly changing environmental conditions. The physiology of insects plays a vital role in the adaptation and competing adjustments in the nature with other species. The mechanism of vision and the involvement of visual pigments, like chromophores particularly in flies, have proved to be landmarks in the field of research. This has been achieved with the discovery of novel pathways involved in the mechanism of pigment development. However, certain visual pigments and their relationship with various chromophores need to be further elaborated. The role of insect pigments in vision, to identify the hosts, prays, and predators, is also discussed. Many naturally occurring pigments of insect origin are continuously being explored for better prospects and human welfare. The abundant availability of insect species all over the world and the never ending task of exploring their potential at morphological, physiological, evolutionary, and genetic levels have a tremendous potential to explore the subject like entomology.

Keywords: insects, chromophore, genetic, ommochrome, pigment, xanthommatin

1. Introduction

Insects represent one of the largest groups of animals on earth, which constitute over 1 million species and still counting (Gross 2006) serving many trophic roles like pests and pollinators in food chains. We are surrounded by a large variety of insects which always attract our attention with their intriguing beautiful color patterns. Pigmentation assists various species of insects in many biological activities, such as camouflage, mimicry, aposematism or warning, selection for



Δ

sex, and communication by signaling [1]. Apart from this, other pigments produced by insects are involved in the metamorphosis, growth, and developmental stages of any colorful insect's life cycle. There are pigments and chromophores [2] that are known to play a vital role in imparting vision to insects for their routine activities. It is interesting and intriguing to know how these colors are formed in insect body. Here, we have addressed the questions related to chromophores found in the eye pigment of insects along with other visual eye pigments.

2. Synthesis of pigments in insects

In insects, the epidermis produces pigments via a series of developmental stages. This pattern formation and synthesis of pigments influence the phenotypes and behavior of insects in one or other way. Most of the insect pigments are either synthesized by insects such as, anthraquinines, pterins, tetrapyrroles, ommochromes, and papiliochromes, or absorbed from the antioxidative carotenoids and flavonoids of their host plants [3]. Apart from imparting body coloration, ommochromes act as visual pigments, melanins protect against ultraviolet radiation, and tetrapyrroles facilitate oxygen transport to cells. Insect pigmentation has been studied in detail by Mollon in most common insect model, *Drosophila melanogaster* [4]. The process of pigmentation in insects occurs in two stages, viz., location or appearance of pigments in space or time and the biological as well as chemical synthesis. These processes are controlled by patterning genes which regulate the distribution of pigments and their effector genes. For instance, in butterfly, *Bicyclus anynana*, a protein called "Engrailed" synthesizes a yellow pigment in later stages which forms the golden ring adult eyespots on the hind wing. While some researchers have revealed that effector genes are responsible for enzymatic pigment production.

2.1. Insect pigmentation: genetics and evolution

Study of pigmentation system is vital for study of links of genetic changes to the evolutionary variation in fitness-related traits of insects [5]. For example, pigmentation of the normal eyes is known to be blocked by majority of mutations in ocelli during the synthesis of brown eye pigment xanthommatin [6]. Mason and Mason [7] have reviewed the current state of comparative biology in context to pigmentation. Advanced studies carried out on genetic analysis of pigmentation in lower vertebrates, mice, and humans elucidate various aspects of development and evolution of the process of pigmentation at different stages. Molecular studies in lower vertebrate pigmentation and a comparative account of genes in different species arising from a common ancestral gene have been fruitful in the study of pigmentation in various insect species [8]. Evolutionary studies between mammals and other vertebrates have revealed significant differences in pigmentation mechanisms between these species. Such data provides an overall view of pigments and their existence across numerous species [7]. Briscoe and Chittka [9] have reviewed the physiological and molecular mechanisms of insect color vision. Recently, role of a marker which is dominantly expressed during insect transgenesis has been elucidated by Takahiro et al. [10].

2.2. Use of pigment in insect

Carotenoids are uniquely involved in functional dynamics of almost all green-colored insects. Heath et al. [11] reviewed the various carotenoids and their derivatives for function and influence of their interactions between their environments, such as vegetation on which they thrive. They also reviewed the biological synthesis as well as structure of these compounds and discussed their roles in various phenomena, such as warning coloration, vision, photoperiodism, and diapause, along with their antioxidative role in signaling. Further, they explored the probable functions of carotenoid derivatives such as strigolactones and apocarotenoids in mediating interactions between insects, plants, fungi, and their parasitoid enemies [11]. Manduca sexta larvae appear blue and green in color when fed on artificial and natural diets (green plants), respectively. The green pigment is made up of two chemicals, namely, biliverdin, which is a blue pigment, and lutein, a yellow pigment. Artificial diet has very little lutein, and Manduca spp. are unable to synthesize lutein on their own and have more of a blue color than their plant fed counterparts. In Manduca sexta, lutein is the only carotenoid absorbed from the diet. This is because special transporters in their gut responsible for absorption of carotenoids recognize only lutein. Strong chemical reagents modify the colors of lepidopterous pigments or in some cases dissolve them out of the wings [12].

2.3. The role of pigmentation in insect vision

There are three types of eyes found in insects, namely, simple, apposition compound, and superposition compound eyes, as shown in **Figure 1**. The color vision of insects can discriminate wavelengths in varying ranges. Honey bee is the best example of this phenomenon.

Adult insects naturally have three simple eyes on the top of their heads which are made up of a lens and an extended retina. Some dorsal ocelli having either tapeta or a mobile iris can view at an angle of 150° or more and as many as 10,000 receptors like those of hunting spiders are present in a single eye. They become more or less out of focus in a condition where the retina and lens are close to each other. Ocelli are horizon detectors which control the response of receptors to variations of intensity, and distance of light perceived by the insect from the environment and contributes to flight equilibrium. The dorsal ocelli of adult locust have a very typical arrangement (**Figure 2**).

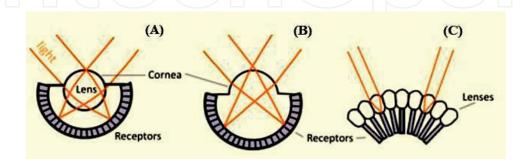


Figure 1. Types of insect eyes (A) simple eye, (B) apposition compound eye, (C) superposition compound eye. (*Source*: [65]).

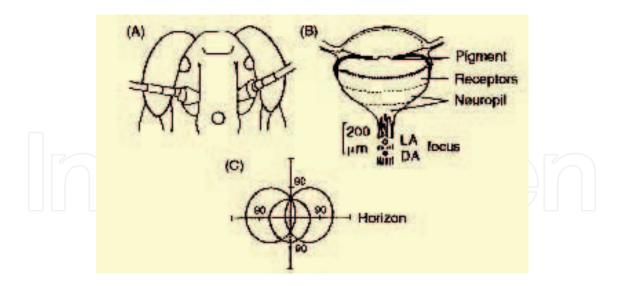


Figure 2. Dorsal ocelli of adult locust: (A) frontal and lateral ocelli on head and (B) section of an ocellus with different layers and positions of the long distance focus behind the receptor tiers in the presence and absence of light. (C) Skyline view of the three ocelli (*source*: http://what-when-how.com/insects/eyes-and-vision-insects/).

The spectral sensitivity in receptors of eyes of honeybees suggests that the visual pigments in insects are rhodopsins, consisting of protein bound to the retina of the eye [13]. Some Lepidopteran insects have color vision with spectral sensitivity suggesting that the eyes contain two photopigments. The photoreceptors form a large part of the eye in sphingid moth, Deilephila elpenor, and most of the screening pigments can be separated out from the receptors [14]. Chemical nature of color vision depends upon the light absorption from the external sources in form of electromagnetic radiation. Typical pigments in the eye act as transducers and convert electromagnetic energy into the chemical energy. This stimulates an impulse within a nerve cell or neuron. All insect visual pigments are produced by retinula cells and stored in the rhabdoms of the compound eyes and ocelli. Only two types of visual pigments, one pigment absorbing green and yellow light and the other absorbing blue and ultraviolet (UV) light, are predominant in insects. However, red color is invisible to insects. Insects have limited color vision only when the frequency of response lies within the UV range. Bichromatic insects having two types of pigment receptors fail to distinguish between single colors and mixture of colors. Trichromatic insects such as honeybees, bumblebees, and most diurnal butterflies possess three types of receptors that are known to have true color vision. It means that they can perceive a complete spectrum of colors and also discriminate between individual colors and color mixtures. Eyes of trichromatic insects have three visual pigments having absorption maxima at UV (360 nm), blue-violet (440 nm), and yellow (588 nm) wave lengths. In any bichromatic insect, both types of receptors are stimulated due to which a combination of UV with yellow, which are at the extremes of insect's visual spectrum, appears as blue green. However, the same combination appears as two separate colors to a trichromatic insect since the receptor of blue-violet remains unstimulated. Bees perceive the unique color combination of UV yellow as equivalent to the purple in humans. Thus, it is the "bee-purple" in bee's color vision. All the peripheral rhabdomeres in ommatidia of Notonecta glauca contain a visual pigment which is sensitive to red color having wavelength of greater than 700 nm. In Notonecta

glauca, on the dorsal region of the eye, both rhabdomeres in a single ommatidium contain either a pigment with absorption maxima at 345 nm or absorption at 445 nm in adjacent rhabdoms. In the ventral part of the eye, central rhabdomeres contain a pigment having maximum absorption in UV range. Variations in spectral absorption in various types of screening pigments were also studied by Schwind et al. [15]. Shozo [16] studied the effect of different intensities of light on the visual pigments and their adaptive evolution. The authors elucidated that critical amino acids involved in spectral orchestration and their interactive effects on spectral shifts are necessary for the molecular function [16].

2.4. Insect eye pigments: pteridines and xanthommatin

Moraes and coworkers [17] were the first to carry out spectral studies for black and red pigment color absorption by insect eye and later compare them with that of *D. melanogaster*. Both the black- and red-type eye forms of *Triatoma infestans* are made up of ommochromes of the xanthommatin type (**Figure 3**). However, eye pigments, namely, pteridines, melanins, and

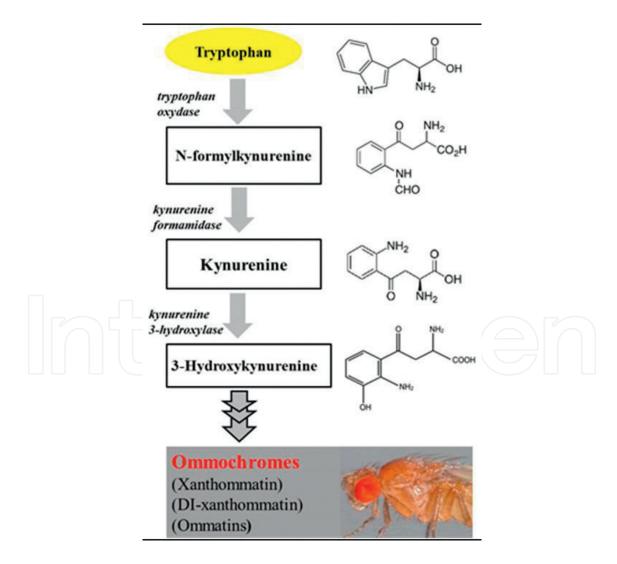


Figure 3. A generalized ommochrome pathway in insects.

ommins, were absent in *T. infestans* unlike *D. melanogaster*. This variation in color of the eye was due to activity of the xanthommatin concentration [17, 18]. Pigments extracted from eyes of wild-type mosquito Anopheles gambiae revealed the presence of the ommatin precursor 3hydroxykynurenine, its transamination derivative xanthurenic acid, and a dark, red-brown pigment spot that probably is composed of two or more low-mobility xanthommatins. No colored or fluorescent pteridines were evident. Some insect colors are a result of mutations that occur in insects during their developmental stages. Mosquitoes homozygous for an autosomal recessive mutation at the red-eye (r) locus have a brick-red-eye color in larvae, pupae, and young adults, in contrast to the almost black color of the wild eye. Mosquitoes homozygous for this mutant allele have levels of ommochrome precursors that are non-distinguishable from the wild type, but the low-mobility xanthommatin spot is ochre-brown in color rather than red-brown as in the wild type. Mosquitoes with two different mutant alleles at the X-linked pink-eye (p) locus, which confers a pink-eye color, and a white eye phenotype (pw) in homozygotes or hemizygous males have normal levels of ommochrome precursors but no detectable xanthommatins. Mosquitoes homozygous for both the r and p mutant alleles have apricotcolored eyes and show no detectable xanthommatins. Both the pink-eye and red-eye mutations involve defects in transport or assembly of pigments in the membrane-bound pigment granules rather than defects in ommochrome synthesis [19]. Ferré et al. [20] analyzed the contents of pigments xanthommatin and dihydro-xanthommatin which are responsible for causing brown eye color and related metabolites' "garnet" gene in the eye color mutants of D. melanogaster. Pteridines the fluorescent metabolites of the xanthommatin pathway responsible for red-eye color were also quantitated. The authors concluded that the synthesis and accumulation of xanthommatin in eyes may be related to pteridine synthesis pathway give rise to isoxanthopterin, drosopterins, and biopterin as final products. Beard et al. [19] reported that pigments in eyes of wild-type mosquito, Anopheles gambiae, show the presence of the ommatin precursor (3-hydroxykynurenine) and a dark red-brown pigment spot composed of two or more low-mobility xanthommatins. Pteridines, however, were found to be absent. They showed the color variations seen in the mutants and compared them with the wild-type eye color. The pink and the red-eye mutations involved defects in the transport into assembly of pigments in the membrane-bound pigment granules rather than defects in ommochrome synthesis [21].

3. Screening pigments and rhodopsins

Pigment cells contain screening pigments which are determinants of eye color in insects. The red-colored screening pigments of eyes of the fly permit stray light to photochemically restore photo-converted visual pigments. Many insect species have dark-colored eyes, with distinctly featured color patterns. A large variety of flies and butterflies were studied by the pioneer Entomologist Stavenga, D. G., to bring forth physical and functional aspects of eye colors in insect color vision [22]. The yellow pigment granules located in photoreceptor cells act like the pupils of the eye which control the light sensitivity and adjust it accordingly. The eyes of most insect possess black screening pigments which protect the photoreceptors from stray light

entering the eyes of insect. Eyes of tabanid flies are strongly metallic in color, due to the multilayered cornea. Such corneal patterns are seen in golden green eyes of deer fly, *Chrysops relictus*. The sensitivity spectrum of photoreceptors with green absorbing rhodopsin is narrowed due to reduction in orange green color transmission of the corneal lens. In contrast, the spectral sensitivity of proximal long wavelength photoreceptors is enhanced by the tapetum in eyes of butterflies and regularized by the pigment granules lining the rhabdom [55]. Kim and colleagues [24] reviewed the peculiarities of the *Drosophila* spp. red-eye pigments and their genes and enzymes involved in its biosynthetic pathway. The retina of the adult tobacco hornworm moth *Manduca sexta* contains three visual pigments, namely, a green sensitive rhodopsin and smaller amounts of blue sensitive and ultraviolet sensitive rhodopsins. Similarly, White and coworkers [63], studied seventeen stages, each stage representing of one to two days of chronological age in the morphological system of *Manduca sexta*. Progressive maturation of the retina in ultrasections was monitored to measure rhodopsin in sections of the retina, and electroretinograms were recorded from stages 8–17.

3.1. Papiliochromes and pterins

Papiliochromes and pterins both present in the ommatidia of eyes in insects are synthesized from amino acids tyrosine, tryptophan, and guanosine triphosphate (GTP), respectively. Chemochromes make the insects attractive by providing striking colors to their appearance and provide functional benefits for the commercially important insects [3].

3.2. Visual pigments of the fruit fly

The vast amount of information available on the fly visual system provides a detailed information regarding other insect species [8]. When light quanta hit upon the visual pigment molecules of the eye, any insect is able to visualize. Hamdorf [26] measured the number of microvilli in the rhabdomere of a blowfly and concluded that a microvillus contains well over 1000 visual pigment molecules, such that, a photoreceptor is made up of approximately 2×10^8 visual pigment molecules [26]. Stavenga and Smakman [27] measured the visual pigment content of Blowfly RI6 photoreceptors in order to determine their spectrum and polarization sensitivities within a particular wavelength range. It is seen in flies that self-screening increases the spectral sensitivity whereas relative UV sensitivity is lowered when the visual pigment content is high. However the electrical response remains unaffected by the amount of visual pigment [27].

4. Synthesis and renewal of visual pigment

The protein opsin which binds to its extraordinary chromophore 3-hydroxyretinal is abundantly present in the visual pigment of the fruit fly [28]. When the rhodopsin state is achieved, the chromophore preexisting in the *cis* configuration gets converted into *trans* isomer after photon absorption. In the next thermostable metarhodopsin state, thermal decay occurs at

different stages in a stepwise manner. Reconversion to rhodopsin occurs in the RI6 principal cell metarhodopsin molecule in houseflies [29] also. Stavenga et al. [30] found a strong variation in peak wavelengths of rhodopsin and metarhodopsin in blowfly and hoverflies, e.g., Eristalis spp. [30]. Photopigments of all animals are composed of a large membrane-spanning protein, the opsin which enfolds the aldehyde of vitamin A, as the chromophore [26, 30, 31]. Chromophores are produced in the presence of retinoids during the process of visual pigment synthesis. Release of chromophore after the intracellular breakdown of opsin and its transport from the visual sense cell to the primary pigment cell in the presence of a light driven isomerase was studied by Schwemer [32]. For the purpose of compass orientation, most insects depend upon the sky polarization pattern, and some insects make use of the sky chromatic contrast [33]. They also identified an opsin of a UV-absorbing visual pigment and studied expression of DRA receptors. The retina of insect eye contains two or more types of cones containing photo pigments with different spectral sensitivities [34]. Light of most visible wavelengths produces a unique pattern of activity among the different cone types. These patterns encode the distribution of wavelengths across the retinal image. When light quanta are absorbed by the chromophores, they change shape and activate the opsin, which then functions as a catalyst for further reactions in the photo receptor. The spectral sensitivity of the photopigment is that of the chromophore, modified by the proximity of the opsin, which disturbs the arrangement of the vitamin A aldehyde. Changes in one amino acid group at critical points in the opsin can significantly alter the spectral sensitivity of the opsin chromophore combination [35]. Because the amino acid sequence of the opsin is determined genetically, mutations through evolution have produced a wide range of photopigments with spectral sensitivities often matched to the ecological niches of the animals [4, 31, 36, 37]. Insects have also developed other strategies for shaping the spectral sensitivities of their ommatidial photoreceptors. Alternating layers of material in the corneal facet can serve as interference filters, permitting a restricted range of wavelengths to reach the photopigment. Neighboring ommatidia can be adapted to different parts of the spectrum by varying the filtering properties of the cornea. The photo receptors of certain flies contain additional pigments which serve as "antennas" facilitating the capture of ultraviolet light and transmitting the energy to rhodopsin to initiate the visual process [38].

4.1. Photoreceptor cell

Goldsmith et al. [39] studied the effect of diet on production of visual pigment. They concluded that carotenoid replacement due to the presence or absence of Vitamin A, promoting production of visual pigment along with chromophore and opsin increment. Providing a deficient chromophore to *Drosophila* spp. and *Calliphora* spp. which are deprived of carotenoid leads to maturation of opsin due to the posttranslationally controlled expression of apoprotein [4, 40–42]. Arikawa et al. [43] demonstrated that there exist distal photoreceptors in the retina of butterflies belonging to genus *Papilio* which exhibits specific spectral sensitivities. A shortwavelength sensitive receptor exists, which may be a UV receptor (normal spectrum), a violet receptor (very narrow spectral bandwidth), a blue receptor, or a green receptor (double peak/ single peak). Ommatidia contain only the violet receptor and single peak receptor, which are capable of emitting fluorescence in the presence of UV light. The fluorescence is emitted from a

pigment which is located at the extreme end of the ommatidium which absorbs UV light, leading to narrow spectral sensitivity of violet receptor and a single peak green receptor [43]. A simple and accurate method was used for measurement of absorbance changes during saturating adaptations of the visual pigment to various monochromatic lights which was based on measurements of difference in spectral amplitudes. The predominant pigment absorbs maximally at rhodopsin and metarhodopsin wavelength [44]. Meinecke and Langer [45] reported that in the noctuid moth *Spodoptera exempta*, each ommatidium regularly contains eight receptor cells belonging to three morphological types: one distal, six medial, and one basal cell for different visual pigments within the eye. Langer et al. [46] also identified three types of visual pigments and their localization in the photoreceptor cells of compound eye of silk moth *Antheraea polyphemus* [46].

4.2. Sensitizing pigment

In flies, visual pigments bind to 3-OH-retinol along with the chromophore 3-OH- retinal [29]. As a result when flies are fed on diet deficient in vitamin A, they demonstrate a low visual sensitivity and show a declined UV sensitivity relative to the blue green peak [47]. The 3-OH-retinol or the sensitizing (antenna pigment) studied by Kirschfeld and his colleagues [48] absorbs UV and upon excitation by a photon transfers the absorbed energy to the chromophore which is later isomerized [48]. Energy transfer occurs from the excited sensitizing pigment to rhodopsin as well as metarhodopsin [49]. A strong enhanced spectral sensitivity in UV spectrum is caused due to the rhodopsin being sensitized by the UV-absorbing antenna pigment [50].

Hamdorf et al. [51] elucidated the in vivo electrophysiological aspect of the rate at which the retinoids get incorporated in the various visual pigments [51]. Role of retinoids in retinal degeneration in *Drosophila* mutant when exposed to various chemicals has also been studied [42]. Minke and Kirschfeld [49] demonstrated that a pigment which is photostable acts as a sensitizer for rhodopsin, and they used membrane potential to measure variations in visual pigment in fruit fly.

4.3. Chromophores

Hamdorf [26] reported behavioral and electrophysiological experiments in honeybee eyes as well as in neuropteran, *Ascalaphus macaronius* [26, 52]. Kashiyama et al. [53] carried out the molecular characterization of visual pigments in *Brachiopoda* spp. and showed that ancestors of *Pancrustacea* spp. and the insect, *Branchiopoda* spp., lineages possessed minimum of five or six types of opsins [53]. Further, Helmut et al. [54] reported the presence of three varieties of visual pigments in the retinal extracts of moth *Antheraea polyphemus*. In many *Drosophila species*, a genetic model for characterizing retinoid-binding proteins was established. It was reported by Tao et al. [55] that PINTA is expressed and is functionally required after the production of vitamin A in the retinal pigment epithelia. It was the first genetic evidence for the retinal pigment cells in visual response in *Drosophila* spp. [55].

4.4. Ommochrome pathway in insects

Ommochromes are biological visual pigments occurring in the eyes of crustaceans and insects, which determine the color of insect eye. Mostly, these are predominantly found in chromophores of cephalopods and spiders. Ommochromes are in the form of pigment granule deposits inside the cells of the hypodermis, just below the cuticle [56]. They are responsible for a wide variety of colors, ranging from yellow, red, and brown to black. Ommatins impart light colors, while combinations of ommatin and ommins are known to impart dark colors [56, 57]. In few insect lineages, ommochromes have special function of coloration of integument and tryptophan secretion. Only in family Nymphalidae, ommochromes are well known as butterfly wing pigments. In order to understand the occurrence of subcellular process during evolution, the development of pigment ommochrome called xanthommatin in the wings of nymphalid butterfly Vanessa cardui was identified and explored. Fragments of ommochrome enzyme genes, "Vermilion" and "Cinnabar," were cloned with the well-known precursor transporter gene called "White." These genes were found to have transcribed at high levels during the development of the wing scale tissue. However, the transcription pattern and adult pigment patterns were not associated with each other. These results indicate that there exists a transcriptional interrelationship between pre-pattern and pigment synthesis in Vanessa cardui [58]. The color of eye shine of some butterflies is determined mainly by the reflectance spectrum of the tapetal mirror and the transmittance spectrum of the photoreceptor screening pigments [23]. Insausti et al. [59] studied the morphological and physiological changes associated with mutation in the red-eyed mutant bug, Triatomine sp. They demonstrated ommochromes as one of the major pigments responsible for coloration of eggs, eyes, and body surface of insects [59]. However, final steps of molecular mechanisms of ommochrome pigment synthesis are not known. Osanai-Futahashi et al. [60] identified the gene involved in egg or eye pigmentation, and it has been identified and characterized in Bombyx and Tribolium species [60] as well.

5. Discussion

Evolutionary questions about process of pigmentation highlight the similarities and differences between various organisms in a framework. Thus, developmental and evolutionary data is useful for creation of a unified view of insect pigment cells and to study its existence across diverse species [7]. Briscoe and Chittka [9] reviewed the physiology, molecular biology, and neural mechanisms of color vision of insects. Studies on phylogeny and analysis at molecular level revealed that the basic bauplan, UV-blue green trichromacy dates back to the Devonian ancestor of all pterygote insects. In addition to exploring these factors, quantification of variance between individual and population of insects and fitness measurements was used to test the adaptiveness of characteristics in insect color systems [9]. The molecular basis of spectrum analyses in vision pigments can be elucidated by conducting experiments to study the adaptation of different insect species to various light conditions with time. To explain the molecular and functional aspect of visual pigment adaptations in a better way, it is necessary to

understand all important molecule exchanges that may be involved in the alignment of spectra and investigate effectiveness of the interactions of spectral shifts [16]. A number of examples of fly and butterfly species possessing dark-colored eyes are known, but distinct colors or patterns are discussed to depict current knowledge available on the physical and functional implications in insect ocular color [61]. Color vision has its greatest value for species that are active during the day when there is abundant light to illuminate objects with different spectral reflectance. Thus, color vision is particularly well developed in various species such as birds, reptiles, and some fishes which trace their evolution through long lines of diurnal ancestors. Humming birds, as well as chickens and pigeons, may have as many as four different cone photo pigments, allowing them to make fine color discriminations over a wide range of wavelengths. Avian cones, like those of certain turtles and amphibians, also contain colored oil droplets which may further refine their spectral selectivity. The oil droplet can act as a filter, limiting the wavelengths that reach the photo pigment. In principle, one can possibly construct a color vision system with one photo pigment and different kinds of oil droplets in different cones, although this strategy does not appear to have been adopted in evolution. The functional significance of the cone oil droplets in birds, turtles, and amphibia still remains unknown [62]. Bernard et al. [63] described the red color absorbing visual pigment of butterflies. Cromartie [64] surveyed the knowledge about chemical nature and biogenesis of the coloring matters of insects. Importantly, the biological significance of important pigments occurring in insects has been mentioned by emphasizing on the remarkable developments [64].

6. Conclusions

Insects are tiny creatures having typical eye features which help them to visualize the world around them and unique pigments which impart beautiful colors to their body parts. The role of color in genetic evolution of many insect species has been studied in the past. The pigments which play a major role in the coloration, especially the pigments that are vital for the vision in insects, have been studied. However, further insight into the same is needed with the use of advanced techniques. The induced and spontaneous mutations related to pigmentation have been investigated in many insect species. The pattern of pigment synthesis and the stages involved during metamorphosis have also been elucidated. The mechanism of vision and the involvement of visual pigments, especially in flies, have proved to be a landmark in the field of research. This has been done by discovery of novel pathways and their detailed studies. However, certain visual pigments and their relationship with various chromophores need elaborate studies to be carried out. The role of insect pigments in vision with respect to identification of hosts and prey-predator interactions for identifying preys is an interesting area of future research. Naturally occurring pigments from insects are being explored for better prospects and welfare of mankind. Their varied applications in areas as edible colors and rich source proteins in food industry can be a subject of future research. The abundant availability of insect all over the world and the never ending task of exploring their potential at the morphological, physiological, evolutionary, and genetic level open up new avenues for a wide and more interesting subject of entomology.

Acknowledgements

Authors acknowledge the authorities of Savitribai Phule Pune University for providing the necessary infrastructural support.

Author details

Tanuja N. Bankar, Mudasir A. Dar and Radhakrishna S. Pandit*

*Address all correspondence to: rspandit@unipune.ac.in

Department of Zoology, Savitribai Phule Pune University, Ganeshkhind, Pune, Maharashtra, India

References

- [1] Alcock J. Animal Behavior: An Evolutionary Approach, 6th ed. Sunderland, MA: Sinauer Associates, Inc.; 1998
- [2] Kirschfeld K. Activation of visual pigment: Chromophore structure and function. In: The Molecular Mechanism of Photoreception. Series Dahlem Workshop Reports. Berlin, Heidelberg: Springer; 1986;34:31-49
- [3] Gulsaz S, Ranjan SK, Pandey DM, Ranganathan R. Biochemistry and biosynthesis of insect pigments. European Journal of Entomology. 2014;111:149164. DOI: 10.14411/eje.2014.021
- [4] Mollon JD. Colour vision: Opsin and options. Proceedings of the National Academy of Sciences of the United States of America. 1999;**96**:4743-4745
- [5] Hoekstra HE. Genetics, development and evolution of adaptive pigmentation in vertebrates. Heredity. 2006;97:222-234. DOI: 10.1038/sj.hdy.6800861
- [6] Vogt K, Kirschfeld K. Chemical identity of the chromophores of fly visual pigment. Die Naturwissenschaften. 1984;71:211-211
- [7] Mason KA, Frost Mason SK. Evolution and development of pigment cells: At the cross-roads of the discipline. Pigment Cell Research. 2000;13:150-155
- [8] Stavenga DG, Schwemer J. Visual pigments of invertebrates. In: Ali MA, editor. Photoreception and Vision in Invertebrates. New York: Plenum; 1984
- [9] Briscoe AD, Chittka L. The evolution of color vision in insects. Annual Review of Entomology. 2001;46:471-510

- [10] Tao W, Craig M. Cellular/molecular rhodopsin formation in drosophila is dependent on the PINTA retinoid-binding protein. The Journal of Neuroscience. 2005;**25**:5187-5194
- [11] Heath JJ, Cipollini D, Stireman JO III. The role of carotenoids and their derivatives in mediating interactions between insects and their environment. Arthropod Plant Interactions. 2013;7:1-20
- [12] Meldola R. Pigments of Lepidoptera. Nature. 1982;45(1174):605-606
- [13] Bernard GD, Remington CL. Color vision in 256 D.G. Lycaena butterflies: Spectral tuning of receptor arrays in relation to behavioral ecology. Proceedings of the National Academy of Sciences of the United States of America. 1991;88:2783-2787
- [14] Höglund G, Hamdorf K, Langer H, Paulsen R, Schwemer J. The photopigments in an insect retina. In: Langer H, editor. Biochemistry and Physiology of Visual Pigments. Berlin Heidelberg New York: Springer; 1973. pp. 167-174
- [15] Shozo Y. Evolution of dim-light and colour vision pigments. Annual Review of Genomics and Human Genetics. 2008;9:259-282. DOI: 10.1146/annurev.genom.9.081307.164228
- [16] Stark WS, Ivanyshyn AM, Greenberg RM. Sensitivity of photopigments of R 1-6, a two-peaked photoreceptor in drosophila, Calliphora and Musca. Journal of Comparative Physiology. 1977;121:289-305
- [17] Moraes AS, Pimentel ER, Rodrigues VL, Mello ML. Eye pigments of the bloodsucking insect, *Triatoma infestans* Klug (Hemiptera, Reduviidae). Brazilian Journal of Biology. 2005; 65:477-481
- [18] Muri RB, Jones GJ. Microspectrophotometry of single rhabdoms in the retina of the honeybee drone (*Apis mellifera*). Journal of Insect Physiology. 2014;**61**:58-65
- [19] Beard CB, Benedict MQ, Primus JP, Finnerty V, Collins FH. Eye pigments in wild-type and eye-colour mutant strains of the African malaria vector *Anopheles gambiae*. Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology. 2002;**188**:337-348
- [20] Ferré J, Silva FJ, Real MD, Ménsua JL. Pigment patterns in mutants affecting the biosynthesis of pteridines and xanthommatin in *Drosophila melanogaster*. Biochemical Genetics. 1986;**24**:545-569. PMID: 3092804
- [21] Beard CB, Benedict MQ, Primus JP, Finnerty V, Collins FH. Eye pigments in wild-type and eye-color mutant strains of the African malaria vector Anopheles Gambiae. The Journal of Heredity. 1995;86:375-380. PubMed PMID: 7560874
- [22] Stavenga DG. Color in the eyes of insects. IUBMB Life. 2013;65(4):334-340. DOI: 10.1002/iub.1145. Epub 2013 Feb 23
- [23] Stavenga DG. Color in the eyes of insects. Journal of Comparative Physiology. A, Neuro-ethology, Sensory, Neural, and Behavioral Physiology. 2002;**188**:337-348. Epub 2002 Apr 13

- [24] Kim H, Kim K, Yim J. Biosynthesis of drosopterins, the red eye pigments of *Drosophila melanogaster*. IUBMB Life. 2013;**65**:334-340. DOI: 10.1002/iub.1145
- [25] Winderickx J, Lindsey DT, Sannocki EDY, Teller DY, Motulsky AG, Deeb SS. Polymorphism in red photopigment underlies variation in color matching. Nature. 1992;356:431-433
- [26] Hamdorf K. The physiology of invertebrate visual pigments. In: Autrum H, editor. Handbook of Sensory Physiology VII/6A. Berlin: Springer; 1979. pp. 145-224
- [27] Stavenga DG. Reflections on colourful ommatidia of butterfly eyes. The Journal of Experimental Biology. 2002;**205**:1077-1085
- [28] Vogt K. Distribution of insect visual chromophores: Functional and phylogenetic aspects. In: Stavenga DG, Hardie RC, editors. Facets of Vision. Berlin, Heidelberg: Springer; 1989. pp. 134-151
- [29] White RH, Brown PK, Hurley AK, Bennett RR. Rhodopsins, retinula cell ultrastructure, and receptor potentials in the developing pupal eye of the moth Manduca sexta. Journal of Comparative Physiology. 1983;150:153-163
- [30] Stavenga DG, Smakman JGJ. Spectral sensitivity of blowfly photoreceptors: Dependence on waveguide effects and pigment concentration. Vision Research. 1986;26:1019-1025
- [31] Jacobs GH. Cone pigments and color vision polymorphism. A comparative perspective in frontiers of visual science. Comparative Colour Vision. Washington, DC: National Academy Press. 1987;176:129-144
- [32] Schwind R, Schlecht P, Langer H. Micro spectrophotometric characterization and localization of three visual pigments in the compound eye of Notonecta glauca L. (Heteroptera). Journal of Comparative Physiology. 1984;154:341-346
- [33] Fabian S, Wakakuwa M, Tegtmeier J, Kinoshita M, Bockhorst T, Arikawa K, Homberg U. Opsin expression, physiological characterization and identification of photoreceptor cells in the dorsal rim area and main retina of the desert locust, *Schistocerca gregaria*. Journal of Experimental Biology. 2014;217:3557-3568. DOI: 10.1242/jeb.108514
- [34] Schwemer J, Spengler E. Opsin synthesis in blowfly photoreceptors is controlled by an l l-cis retinoid. In: Rigaud JL, editor. Structures and Functions of Retinal Proteins. 1992. pp. 277-280
- [35] Wittkopp PJ, Beldade P. Development and evolution of insect pigmentation: Genetic mechanisms and the potential consequences of pleiotrophy. Review Seminars in Cell and Development Biology. 2009;20:65-71
- [36] Goldsmith T. Optimization, constraint and history in the evolution of eyes. Quart. Rev. Biol. 1990;65:281-322
- [37] Osanai-Futahashi M, Tatematsu K, Yamamoto K, Narukawa J, Uchino K, Kayukawa T, Shinoda T, Yutaka B, Tamura T, Sezutsu H. Identification of the *Bombyx* red egg gene reveals the involvement of a novel transporter family gene in the late steps of the insect

- ommochrome biosynthesis pathway. Membrane Biology: Journal of Biological Chemistry. 2012. published online April 2, 2012:**287**
- [38] Menzel R. Spectral sensitivity and colour vision in invertebrates. In: Autrum H, editor. Handbook of Sensory Physiology VII/6A. Berlin: Springer; 1979. pp. 501-580
- [39] Goldsmith TH, Barker RJ, Cohen CE. Sensitivity of visual receptors of carotenoid-depleted flies: A vitamin A deficiency in an invertebrate. Science. 1964;146:665-667
- [40] Isono K, Tanimura T, Oda Y, Tsukahara Y. Dependency on light and vitamin a derivates of the biogenesis of insect retinal pigments 3-hydroxyretinal and visual pigment in the compound eye of *Drosophila melanogaster*. The Journal of General Physiology. 1988;**92**:587-600
- [41] Reed RD, Nagy LM. Evolutionary redeployment of a biosynthetic module: Expression of eye pigment genes vermilion, cinnabar, and white in butterfly wing development. Evol. Dev. 2005;7(4):301-311
- [42] Schwemer J. Visual pigment renewal and the cycle of the chromophore in the compound eye in the blowfly. In: Wiese K, Gribakin EG, Popov AV, Renninger G, editors. Sensory Systems of Arthropods. 1993. pp. 54-68
- [43] Arikawa K, Mizuno S, Scholten DGW, Kinoshita M, Seki T, Kitamoto J, Stavenga DG. An ultraviolet absorbing pigment causes a narrow-band violet receptor and a single peaked green receptor in the eye of the butterfly *Papilio*. Vision Research. 1999;**39**:1-8
- [44] Nicol JAC. Studies on the eyes of fishes. Vision in Fishes: NATO Advanced Study Institute Series. 1975;1:579-607
- [45] Meinecke CC, Langer H. Localization of visual pigments within rhabdoms of the compound eye of *Spodoptera exempta* (Insecta: Noctuidae). Cell and Tissue Research. 1984;**238**: 359-368
- [46] Langer H, Schmeinck G, Friedericke A. Identification and localization of visual pigments in the retina of the moth, *Antheraea polyphemus* (Insecta Saturnidae). Cell and Tissue Research. 1986;**245**:81-89
- [47] Stavenga DG. Insect retinal pigments: Spectral characteristics and physiological functions. Pigment of Eye. 1982;11:231-255
- [48] Kirschfeld K, Franceschini N, Minke B. Evidence for a sensitizing pigment in fly photoreceptors. Nature. 1977;**269**:386-390
- [49] Minke B, Kirschfeld K. The contribution of a sensitizing pigment to the photosensitivity spectra of fly rhodopsin and metarhodopsin. The Journal of General Physiology. 1979;73: 517-540
- [50] Hardie RC. The photoreceptor array of the dipteran retina. Trends in Neurosciences. 1986; 9:419-423
- [51] Hamdorf K, Hochstrate P, Höglund G, Moser M, Sperber S, Schlecht P. Ultra-violet sensitizing pigment in blowfly photoreceptors Rl-6; probable nature and binding sites. J. comp. Physiol. A. 1992;171:601-615

- [52] Hamdorf K, Schwemer J, Gogala M. Insect visual pigment sensitive to ultraviolet light. Nature. 1971;**231**:458-459
- [53] Kashiyama K, Seki T, Numata H, Goto SG. Molecular characterization of visual pigments in Branchiopoda and the evolution of opsins in Arthropoda. Mol Biol Evol. 2009;2: 299-311. DOI: 10.1093/molbev/msn251
- [54] Helmut L, Schmeinck S, Antonerxleben F. Identification and localization of visual pigments in the retina of the moth, *Antheraea polyphemus* (Insecta, Saturniidae). Cell and Tissue Research. 1986;245:81-89
- [55] Tearle R. Tissue specific effects of ommochrome pathway mutations in Drosophila melanogaster. Genetical Research. 1991;57:257-266. PubMed PMID: 1909678
- [56] Ozaki K, Nagatani H, Ozaki M, Tokunaga F. Maturation of major Drosophila rhodopsin, ninaE, requires chromophore 3-hydroxyretinal. Neuron. 1993;**10**(6):1113-1119
- [57] JRM C, Casas M. The multiple disguises of spiders: A: Web color and decorations, body color and movement. Philosophical Transactions of the Royal Society B: Biological Sciences. 2009;364:471-480. DOI: 10.1098/rstb.2008.0212. PMC 2674075.PMID 18990 672
- [58] Schwemer J. Visual pigments of compound eyes—Structure, photochemistry, and regeneration. In: Stavenga DG, Hardie RC, editors. Facets of Vision. Berlin, Heidelberg: Springer; 1989; pp. 134-151
- [59] Insausti TC, Le Gall M, Lazzari CR. Oxidative stress, photo damage and the role of screening pigments in insect eyes. Journal of Experimental Biology. 2013;216:3200-3207. DOI: 10.1242/jeb.082818. PMID: 23661779
- [60] Oxford GS, Gillespie RG. Evolution and ecology of spider colouration. Annual Review of Entomology. 1998;43:619-643. DOI: 10.1146/annurev.ento.43.1.619. PMID 15012400
- [61] Takahiro O, Junya H, Keiro U, Ryo F, Toshiki T, Teruyuki N, Hideki S. A visible dominant marker for insect transgenesis. Nature Communications. 2015;3:1-9. DOI: 10.1038/ncomms 2312
- [62] Goldsmith TH, Collins JS, Licht S. The cone oil droplets of avian retinas. Vision Research. 1984;24:1661-1671
- [63] Bernard GD. Red-absorbing visual pigment of butterflies. Science. 1979;203:1125-1127
- [64] Cromartie RIT. Insect pigments. Annual Review of Entomology. 1959;4:59-76. DOI: 10.1146/annurev.en.04.010159.000423
- [65] Land M. The optical structures of animal eyes. Current Biology 2005;**15**:319-323. DOI: 10.1016/j.cub.2005.04.041