DC-I, Semester-II
Paper No:- III-Diversity and Evolution of non Chardata-II
Lesson: Vision in Arthropoda
Lesson Developer: Sarita Kumar
College/ Department: Zoology, Acharya Narendra Dev College

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Introduction

Arthropods possess various kinds of sensory structures which are sensitive to different kinds of stimuli. These structures either protrude from the cuticle, or sometimes lie within or beneath it. These modifications of arthropod exoskeleton which contain sensory neurons and are sensitive to environmental information are called **sensilla** (sing: sensillum). The sensilla may be in the form of hair, bristles, setae, slits, pegs, pits etc.

Some of the receptors present in the arthropod body are as follows.

a) Chemoreceptors: sensitive to chemical stimulus
b) Mechanoreceptors: sensitive to movement
c) Tactoreceptors: sensitive to touch
d) Olfactoreceptors: sensitive to smell
e) Audioreceptors: sensitive to sound
f) Photoreceptors: sensitive to light

Value Addition: Did You Know??
Heading Text: Slit Sensilla in Spiders
Body Text: The slit sensillum is a small mechanoreceptor organ in the exoskeleton of spiders. It detects strain due to forces experienced by the animal. As the name indicates, a slit sensillum is a small groove in the exoskeleton which deforms under stress, and these deformations are detected by neurons. Slit sensilla may occur singly, in widely spaced groups of varying alignment, or in tightly clustered parallel groups, with the last being called a 'lyriform organ'.
Source: http://en.wikipedia.org/wiki/Slit_sensilla

Most of the arthropods possess eyes, which can vary in number, structure and complexity. The eyes of arthropods may be in the form of photoreceptors, simple eyes or compound eyes.

Simple Eyes in Arthropods - Ocelli

The word **ocelli** is derived from the Latin word *ocellus* which means little eye. Ocelli are simple eyes which comprise of single lens for collecting and focusing light.

Arthropods possess two kinds of ocelli

a) Dorsal Ocelli
b) Lateral Ocelli (Stemmata)

Dorsal Ocellus

Dorsal ocelli are found on the dorsal or front surface of the head of nymphs and adults of several hemimetabolous insects. These are bounded by compound eyes on lateral sides. Dorsal ocelli are not present in those arthropods which lack compound eyes.

- Dorsal ocellus has **single corneal lens** which covers a number of sensory rod-like structures, rhabdome.
- The ocellar lens may be curved, for example in bees, locusts and dragonflies; or flat as in cockroaches.
- It is sensitive to a wide range of wavelengths and shows quick response to changes in light intensity.
- It cannot form an image and is unable to recognize the object.

(a)

(b)

Fig 1. Head of (a) *Polistes* and (b) another wasp with three ocelli

Source: http://en.wikipedia.org/wiki/Simple_eye_in_invertebrates

Lateral Ocellus - Stemmata

Lateral ocelli, known as **stemmata** are the only eyes in the larvae of holometabolous and certain adult insects such as spring tails, silver fish, fleas and stylops.

- These are called lateral eyes because they are always present in the lateral region of the head.
- The number of lateral ocelli varies from one to six on each side.
- They are structurally similar to dorsal ocelli except that they have a biconvex lens and a crystalline cone beneath the cornea with less number of rhabdomes.
- These ocelli are sensitive to light intensity and thus capable of detecting outlines and movement of nearby objects and organisms.

Fig 2. Head of a caterpillar with stemmata

Source: http://commons.wikimedia.org/wiki/File:Caterpillar_head_morphology.PNG

Value Addition: Interesting to Know…
Heading Text: Single Sensor Hypothesis
Body Text: In 1978, Wilson proposed a hypothesis of ocellar function based on locust ocelli, referred to as the "single-sensor" hypothesis. It suggests that the ocelli do not resolve spatial details of the environment: instead, each ocellus functions as a highly sensitive light detector of illumination levels from a wide region of visual space. Their large aperture and field of view suggest that they are designed to detect overall brightness while minimizing the effect of small objects in the visual field. According to another theory ocelli are used to assist in maintaining flight stability because of their wide fields of view and high light-collecting ability.
Source: http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3928595/#!po=98.5714

Compound Eyes in Arthropods

A number of arthropods possess eyes which are made up of hundreds/thousands of long, cylindrical photoreceptor units. Such eyes are termed as **compound eyes**. Each unit is called an **ommatidium** (pl; ommatidia) and is capable of forming a separate image, independent of other ommatidium. Thus, image formed is a combination of inputs from a number of ommatidia.

Fig 3. Head of Robber Fly with Compound eyes

Source: http://commons.wikimedia.org/wiki/File:Opo_Terser_-_Compound_Eyes_of_a_Robber_Fly_-_%28Holcocephala_fusca%29_%28by%29.jpg

Value Addition:

Heading Text: Evolution of Compound Eye

Body Text: On the basis of ommatidial focusing structures and the arrangement of receptor cells the researchers have shown that the evolution of compound eyes proceeded largely independently along at least two lineages from very primitive ancestors.

A common ancestor of insects and crustaceans is likely to have had ommatidia with focusing crystalline cones, and colour and/or polarization vision. In contrast, the compound eyes in myriapods and chelicerates are likely to date back to ancestors with corneal lenses and probably without the ability to discriminate colour and polarization.

Source: Nilsson D-E and Kelber A (2007) A functional analysis of compound eye evolution. *Arthropod Structure & Development*, 36:373–385.

Structure of an Ommatidium

Each ommatidium consists of the following parts:

a) Cornea:

- The outer surface of each ommatidium is **convex** and is covered by the transparent cuticle. It forms the cornea and functions as a **biconvex lens**.
- The external surface of cornea is generally hexagonal but sometimes square in shape and is called a **corneal facet**. Large number of facets gives an interesting appearance to the compound eyes, which often looks like a graph paper.
- Cornea, being cuticular in nature, sheds during each moult. New cornea is secreted by **corneagen cells** which are present beneath each facet.

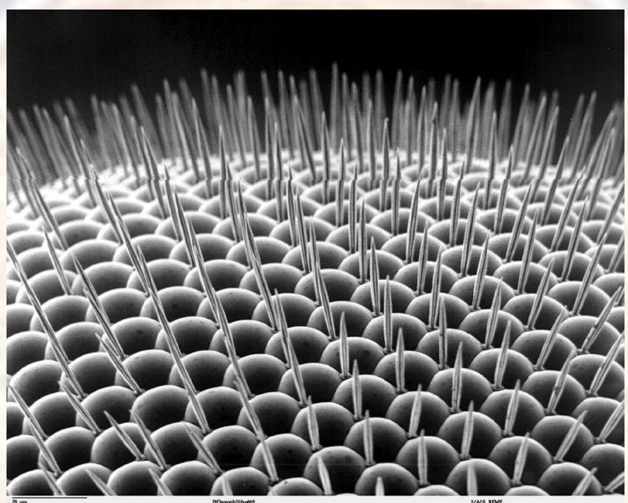

Fig 4. Compound eye of *Drosophila* showing corneal facets

Source: http://commons.wikimedia.org/wiki/File:Drosophilidae_compound_eye_.jpg

b) Crystalline Cone:

- The corneagen cells are followed by a long, cylindrical or tapering, transparent **crystalline cone**.
- It is surrounded by 4-6 elongated cone cells, called **vitrellae,** with long and tapering ends.
- Crystalline cone functions as the **second lens** and helps to **focus light** upon the photoreceptors present in the ommatidium.

The region of each ommatidium, from cornea till the end of cone cells, is termed as **dioptrical region**.

c) Photoreceptor Unit:

- Basal end of cone cells of the ommatidium lie upon a translucent cylinder, called **rhabdome**.
- Rhabdome receives light and functions as a single photoreceptor unit forming an image.
- Rhabdome is surrounded by 7-8 light-sensitive photoreceptor cells, **retinular cells**. These are arranged in a radial pattern like the sections of an orange.
- Each retinula cell rests upon a **basement membrane** and extends into an **axon**.
- The bundle of 7-8 axons leaving each ommatidium is further connected to the neurons of **optic ganglion** which is connected to the brain through **optic nerve**.

Rhabdome and retinular cells collectively form the **receptor region** of the eye.

d) Pigment Cells:

- Each ommatidium is separated from its neighbouring ommatidia by certain **pigment cells**.
- The primary pigment, **iris**, is present in the proximal region of the ommatidium surrounding the tapering ends of the cone cells.
- The secondary pigment, **retinal pigment**, surrounds the rhabdome and retinal cells in the distal region of the ommatidium.
- These pigments are movable and can migrate centrally or distally depending upon the light intensity.

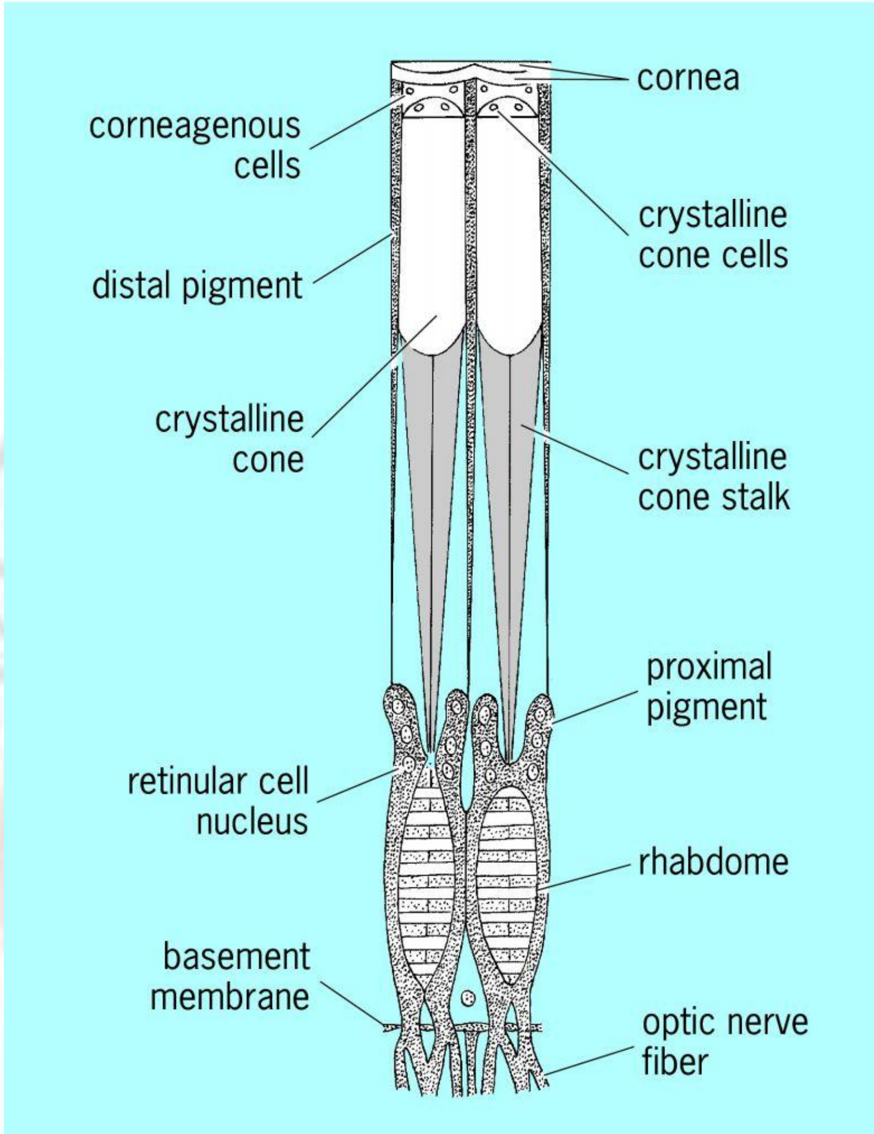

Fig 5. Detailed Structure of an Ommatidium

Source: http://encyclopedia2.thefreedictionary.com/a+%27s-eye+view

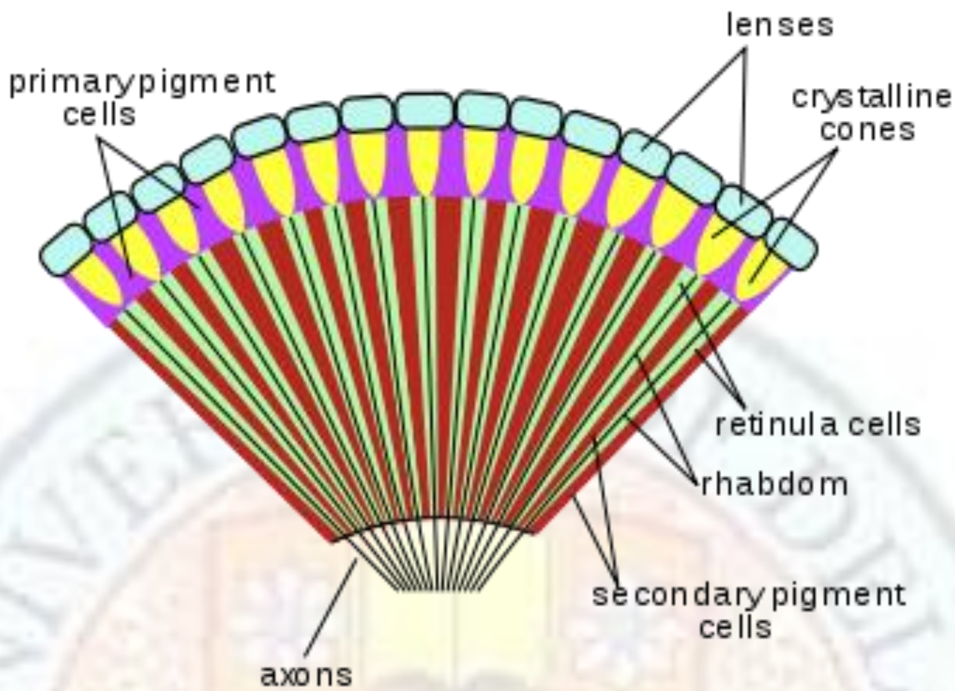

Fig 6. L.S. of a Compound eye showing ommatidia

Source: http://en.wikipedia.org/wiki/File:Insect_compound_eye_diagram.svg

Value Addition: Video
Heading Text: Structure and Function of an Ommatidium
Body Text: The videos describe the detailed structure and functions of the visual unit, an ommatidium, of the compound eye and explains the vision in arthropods.
Source: https://www.youtube.com/watch?v=TU6bgQnTi18 https://www.youtube.com/watch?v=Ix1ubH88o5Q

Image Formation

Compound eyes form image with the help of inputs received from ommatidia. Each ommatidium forms a separate image of a small part of the object. Thus, the image formed consists of several pieces and is crude. This type of vision is called **mosaic vision**.

Compound eyes of arthropods can form two kinds of image depending on the intensity of light:

a) Apposition image
b) Superposition image

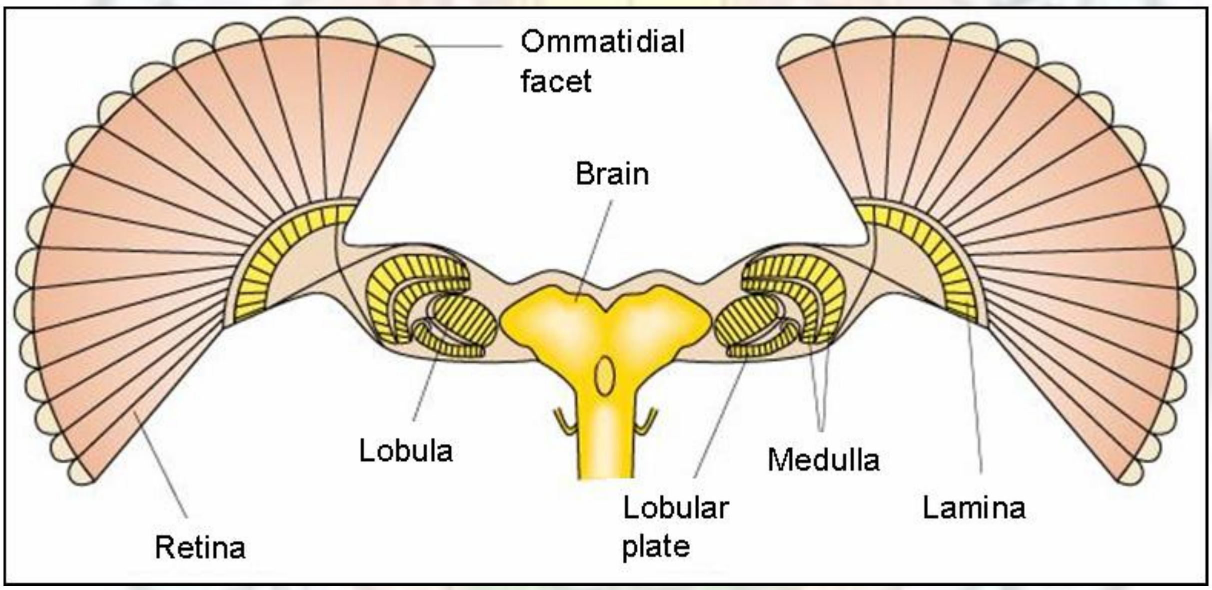

Fig 7. Stalked Compound eyes connected to the brain

Source: http://images.lingvistika.org/w/images/f/f9/Compound_eye.jpg

Apposition Image

The compound eyes form apposition image in the bright light.

- In bright light, both proximal and distal pigments extend and act as a screen to prevent light rays from passing from one ommatidium to another.

- The light rays remain restricted to the axial region of the crystalline cone and rhabdomes.
- As a result, only those rays which fall perpendicularly on the cornea and pass through rhabdome form the point of an image. The rays which fall obliquely on the cornea are absorbed by the pigment and do not produce any visual effect.
- Thus, each ommatidium responds to a patch of light from the visual field and overlaps little with the neighbouring ommatidia forming a point of an image.
- The final image is formed by combining all these points formed by the stimulated ommatidia.
- This is, therefore, mosaic vision as it results from small pieces put together.

Apposition eyes are the most common form of eye, and are presumably the ancestral form of compound eye. They are found in all arthropod groups.

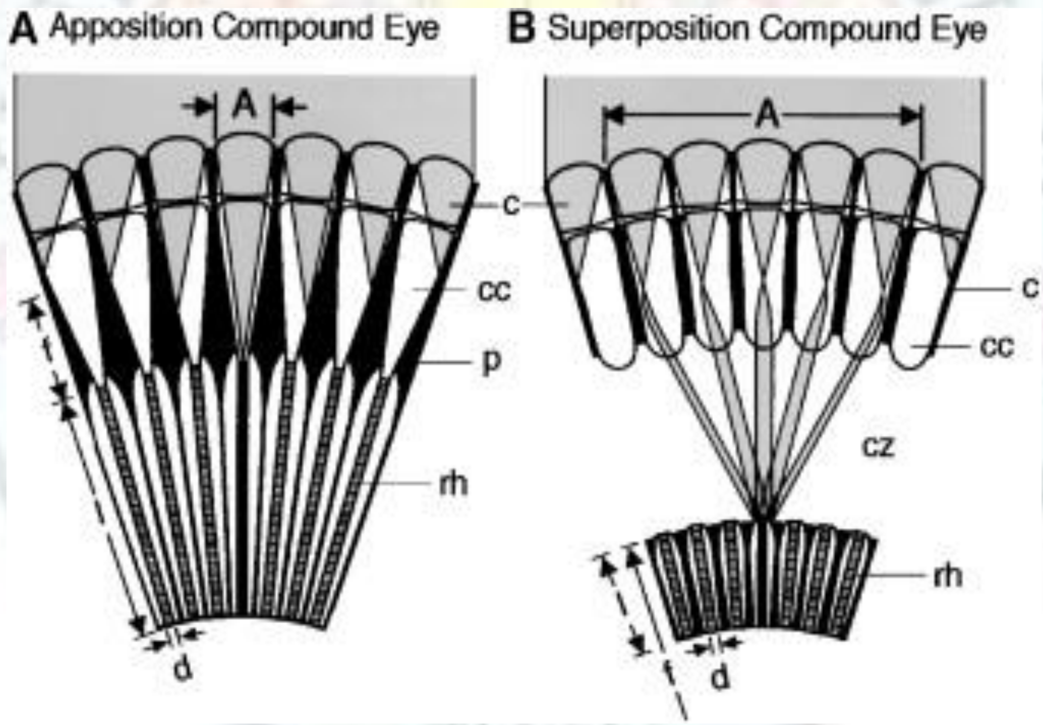

Fig 8. Apposition and Superposition Image formed by Compound Eyes
c: Cone cell, cc: Crystalline cone, p: pigment, rh: Rhabdome, d: distance

Source: http://www.scholarpedia.org/article/File:Eye_types_basic.jpg

Superposition Image

The superposition image is formed in the dim light.

- In weak light, both proximal and distal pigments retract. The ommatidia do not remain optically isolated and the light rays can pass from one ommatidium to another.
- As a result, the oblique rays as well those which fall perpendicularly on the cornea and pass through rhabdome form the point of an image.
- Thus, each ommatidium responds to the light rays which had entered through different corneal facets.
- The final image is continuous formed by overlapping of the adjacent points of images.

Apposition Eye Vs Superposition Eye

The compound eyes of many arthropods are able to adapt both bright and weal light, such as in prawn. These species thus can see in daylight as well as in night. However, in several arthropods, the eyes are adapted and fixed for working under only one condition. Therefore, compound eyes can be classified as apposition eye and superposition eye.

Table 1: Difference between Apposition Eye and Superposition Eye

Features	Apposition Eye	Superposition Eye
Light intensity	Stimulated by strong light intensity	Stimulated by low intensity of light
Screening pigment	Well developed	Present but may be reduced or absent in some
Length of crystalline cone	Approximately equal to the focal length	Twice as long as the focal length
Space between cone and upper end of abdomen	Absent, both contiguous	Considerable space permitting light rays to cross from crystalline cone of one ommatidium to rhabdome of another
Retinular cells	Long extending till the basal membrane of retina	Shorter restricted to the base of ommatidium

Light rays	Enter through single ommatidium through axial region	Enter through several ommatidia through all regions
Examples	Diurnal species, such as butterfly	Nocturnal species, such as cockroaches, moths

Value Addition: Fact File!!

Heading Text: Colour Vision in Arthropods

Body Text: Many arthropods exhibit colour vision. Honey bee and bumblebees have trichromatic colour vision, which is insensitive to red but sensitive to ultraviolet. The colour vision in bees helps them to choose the types of flowers that they visit. The hymenopteran insects excluding ants (i.e., bees, wasps and sawflies) have three types of photoreceptors, with spectral sensitivities similar to the honeybees. *Papilio* butterflies possess six types of photoreceptors and may have pentachromatic vision. The most complex colour vision system in animal kingdom has been found in stomatopods (such as the mantis shrimp) with up to 12 different spectral receptor types thought to work as multiple dichromatic units.

Source: http://en.wikipedia.org/wiki/Color_vision

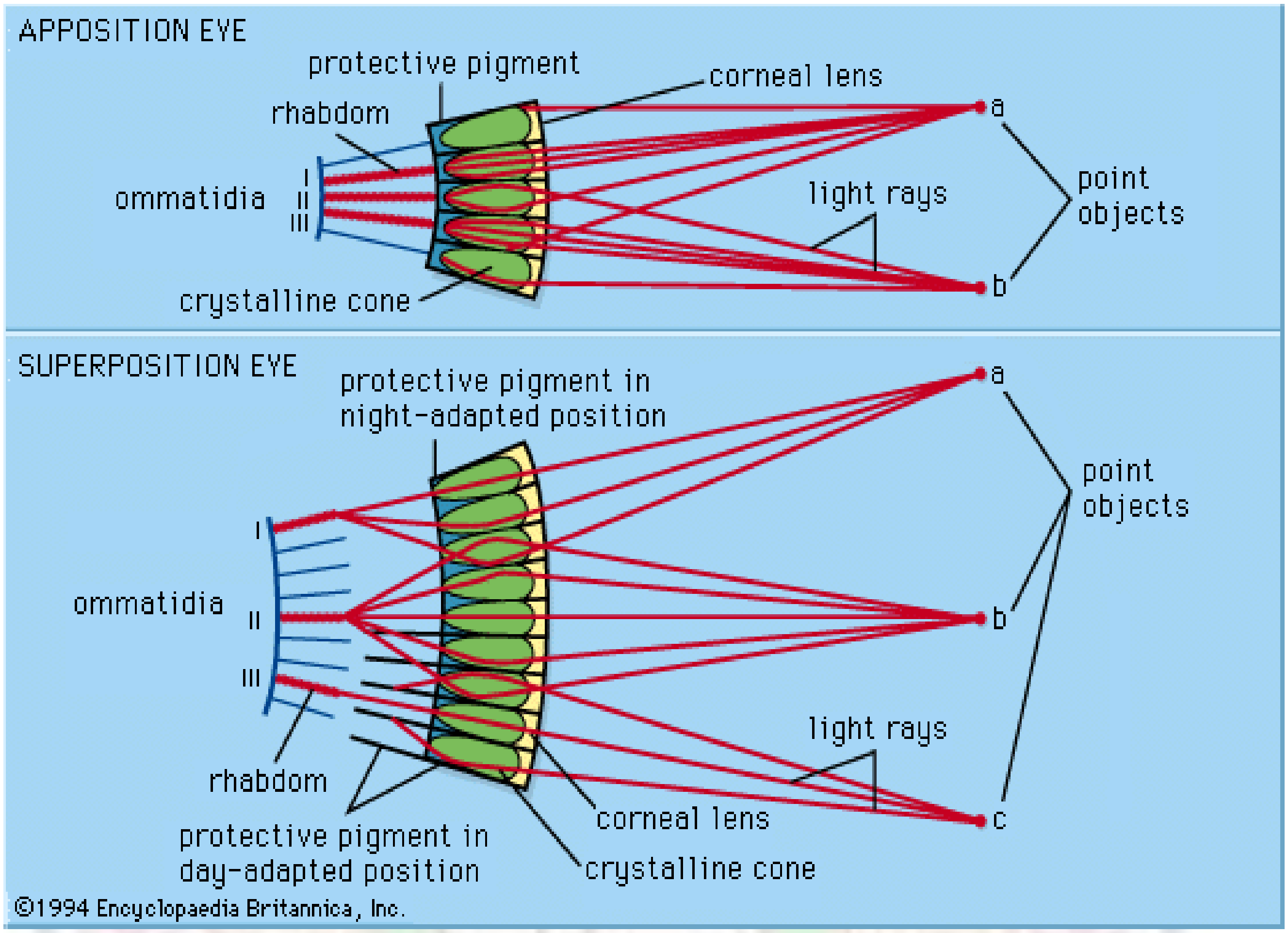

Fig 9. Apposition and Superposition Eyes

http://bright-visions.blogspot.in/2010/09/types-of-eyes.html

Advantages and Disadvantages of Compound Eyes

Compound eyes have many advantages and disadvantages over human eyes.

Advantages

(a) The compound eyes have a convex corneal surface which results in a wide visual field. In crustaceans, eyes can cover an arc of 180° or even more.

(b) Compound eyes can detect even movements very easily. A slight movement in the point of light results in the corresponding shift in the ommatidia.

(c) Eyes of many diurnal arthropods possess high flicker fusion frequency because of which they perceive an object as a succession of separate images, instead of a single image. This helps them to detect motion readily.

Value Addition: Interesting Fact!!
Heading Text: Characteristics of Bee Eyes
Body Text: Honey bee see flowers differently than humans. They cannot see red, but they can see ultraviolet flower coloration that human eyes cannot detect. Their eyes also have a high flicker-fusion frequency, which means they can easily detect rapidly moving objects. If a honey bee were to view a movie, it would look like a slide show. The structure and function of honey bee eyes also dramatically affects their navigation. One reason is that honey bees cannot actually see the sun in the sky. Also, to a bee, anything more than about 2 meters away is just a blur.
Source: http://utahpests.usu.edu/htm/utah-pests-news/up-winter-2012/honey-bee-navigation

Disadvantages

(a) The image formed by the compound eyes is very crude. An insect could see a row of closely spaced bar as a continuous horizontal bar.

(b) The compound eyes do not provide good visual effect in distance vision.

(c) Compound eyes possess poor resolving power because of the small-sized numerous lenses. Therefore, they cannot pick up details of an object as human eyes can do. For example, when a human eye can make out full details of a human hand, a compound eye can only make out an outline of the hand.

Value Addition: Did You Know??
Heading Text: Bees can learn to discriminate human faces
Body Text: Researchers have shown that honeybees, *Apis mellifera*, are capable of complex visual processing and learning tasks. With a small fraction of mammalian neural complexity, honeybees are capable of discriminating face-like visual stimuli; both between face-like and non-face-like stimuli and between variations of face like stimuli. They are thus capable of visually discriminating and remembering one human face from another. This behavior is a clue about the bee's underlying visual processing capacities and **configural** processing. It shows that honeybees are able to perceive and learn, not just the individual components of a visual stimulus, but the interrelationships between them.
Source: Avarguès-Weber et al. (2010). Configural processing enables discrimination and categorization of face-like stimuli in honeybees. *Journal of Experimental Biology,* 213: 593-601.

Value Addition: Video
Heading Text: Visual sensitivity in Insects
Body Text: The video depicts how an insect views the landscape from within the compound eye and visual sensitivity.
Source: https://www.youtube.com/watch?v=F0MqmNUz6WI

Summary

- Arthropods possess various kinds of sensory structures sensitive to different kinds of stimuli.

- The modifications of arthropod exoskeleton which contain sensory neurons and are sensitive to environmental information are called sensilla.

- Ocelli are simple eyes which comprise of single lens for collecting and focusing light.

- Dorsal ocelli have single corneal lens and are found along with the compound eyes on the dorsal or front surface of the head of nymphs and adults of several hemimetabolous insects.

- Lateral ocelli, known as stemmata are present in the lateral region of the head and are the only eyes in the larvae of holometabolous and certain adult insects.

- Compound eyes are made up of hundreds/thousands of long, cylindrical photoreceptor units, called ommatidia.

- Each ommatidium is covered by a convex and transparent cuticle which forms the cornea and functions as a biconvex lens.

- The external surface of cornea is generally hexagonal but sometimes square in shape and is called a corneal facet.

- New cornea is secreted by corneagen cells present beneath each facet.

- Crystalline cone is long and transparent present beneath the corneagen cells and surrounded by 4-6 elongated cone cells, vitrellae. It functions as the second lens and helps to focus light upon the photoreceptors.
- Photoreceptor unit consists of rhabdome surrounded by 7-8 light-sensitive photoreceptor retinular cells.

Vision in Arthropoda

- The retinula cells rest upon a basement membrane and extends into an axon which is connected to the neurons of optic ganglion.

- Each ommatidium is separated from its neighbouring ommatidia by certain pigment cells – iris in proximal region and retinal in distal region.

- Each ommatidium forms a separate image of a small part of the object. Thus, the image formed consists of several pieces and is mosaic.

- In bright light, arthropods form apposition image which consists of separate pieces due to the optical isolation of two ommatidia by extension of pigments.

- In dim light, arthropods form superposition image which consists of overlapped pieces as two ommatidia are not optically isolated due to the retraction of pigments.

- Compound eyes are advantageous as they can detect movement very rapidly, have high flicker fusion frequency and wide visual field. However, they form a crude image of low resolution and are thus, not good for distance vision.

Exercise/Practice

Q1. Differentiate between

a) Apposition image and Superposition image
b) Dioptrical region and Receptor region
c) Cone cells and Retinular cells
d) Crystalline cone and Rhabdome

Q2. Name the following

a) Receptors sensitive to movement
b) Modifications of arthropod exoskeleton which contain sensory neurons
c) Image formed by compound eyes in dim light
d) Compound eyes in moths
e) Ocelli with single corneal lens
f) Pigment present in the proximal region of an ommatidium
g) Second lens of compound eye

Q3. Answer the following questions in short.

(a) Differentiate between dorsal ocelli and lateral ocelli.
(b) Write the differences between the two kinds of images formed by compound eye.
(c) How are eyes of moths and cockroaches adapted to see in the dark?
(d) Name the two pigments present in the compound eye and write their functions.

Q4. Answer the following questions in detail.

(a) What are the characteristic features of a compound eye?
(b) 'Crustaceans can see along 180 degrees and even more' Justify the statement.
(c) Describe the structure of a compound eye with the help of diagrams.
(d) Explain the working of compound eye under different light intensities.
(e) Discuss the advantages and disadvantages of compound eye over human eye.

Glossary

Apposition Image: Image formed in the bright light which consists of separate pieces due to the optical isolation of two ommatidia by extension of pigments.

Compound Eye: Eye made up of hundreds/thousands of long, cylindrical photoreceptor units.

Corneagen cells: Cells that secrete cornea after moulting.

Corneal Facet: External surface of cornea in compound eye which is generally hexagonal but sometimes square in shape.

Crystalline Cone: Long, cylindrical lens which helps to focus light upon the photoreceptors present in the ommatidium.

Dorsal Ocelli: Ocelli found on the dorsal or front surface of the head of nymphs and adults of several hemimetabolous insects.

Iris: Pigment present in the proximal region of the ommatidium.

Lateral Ocelli: Ocelli present in the lateral region of the head in the larvae of holometabolous and certain adult insects.

Ocelli: Little eyes consisting of single lens.

Ommatidium: A unit of compound eye capable of forming a separate image, independent of other ommatidium.

Retinal Pigment: Pigment present in the distal region of the ommatidium.

Rhabdome: Translucent cylinder which receives light and functions as a single photoreceptor unit forming an image.

Sensilla: Modifications of arthropod exoskeleton which contain sensory neurons and are sensitive to environmental information.

Superposition Image: Image formed in dim light which consists of overlapped pieces as two ommatidia are not optically isolated due to the retraction of pigments.

References/ Bibliography/ Further Reading

Suggested Readings

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- Ruppert, Fox and Barnes (2006) Invertebrate Zoology. A functional Evolutionary Approach, 7th Edition, Thomson Books/Cole
- Barnes, R.S.K., Calow, P., Olive, P. J. W., Golding, D.W. and Spicer, J.I. (2002). *The Invertebrates: A New Synthesis,* III Edition, Blackwell Science
- Barrington, E.J.W. (1979). *Invertebrate Structure and Functions*. II Edition, E.L.B.S. and Nelson

Useful Web Links

http://en.wikipedia.org/wiki/Simple_eye_in_invertebrates
http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3928595/#!po=98.5714
http://en.wikipedia.org/wiki/Color_vision
http://utahpests.usu.edu/htm/utah-pests-news/up-winter-2012/honey-bee-navigation