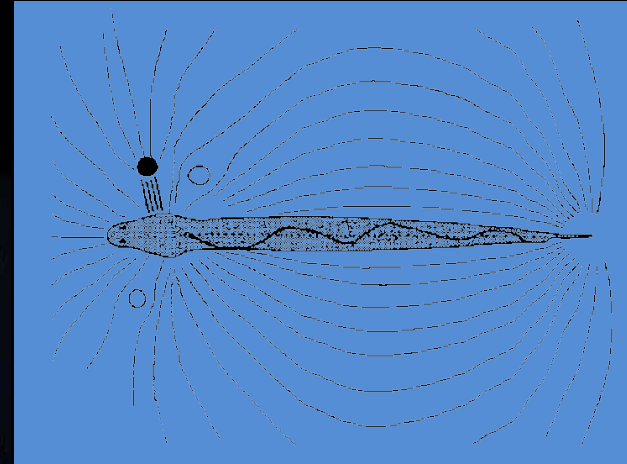
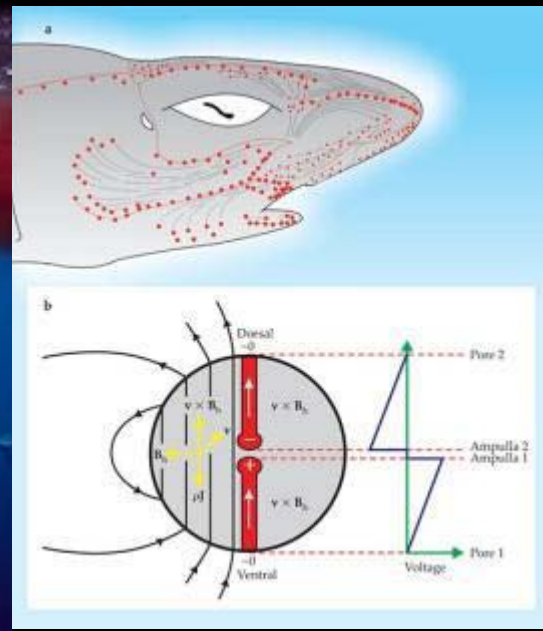


FISH SENSORY SYSTEMS

2nd year – 2011



Introduction

What are the FUNCTIONS of sensory systems?

Sensory systems PROVIDE ORGANISMS WITH INFORMATION from their EXTERNAL ENVIRONMENTS allowing them to MAKE APPROPRIATE RESPONSES to stimuli

SENSORY CELLS act as SIGNAL TRANSDUCERS - they RECEIVE STIMULI in one form and CONVERT THEM TO BIOLOGICAL SIGNALS that can be transmitted VIA THE NERVOUS SYSTEM

There are five categories of sensory systems in fishes:

- VISION (2 lectures)
- MECHANORECEPTION (1 lecture)
- CHEMORECEPTION (1 lecture)
- ELECTRORECEPTION (1/2 lecture)
- MAGNETORECEPTION (1/2 lecture)

Vision

Outline:

Introduction

Optical properties of water

Reflection, refraction and absorption

Snell's law and Snell's window

Anatomy of the eye

Cornea

Iris

Lens

Sclera

Choroid

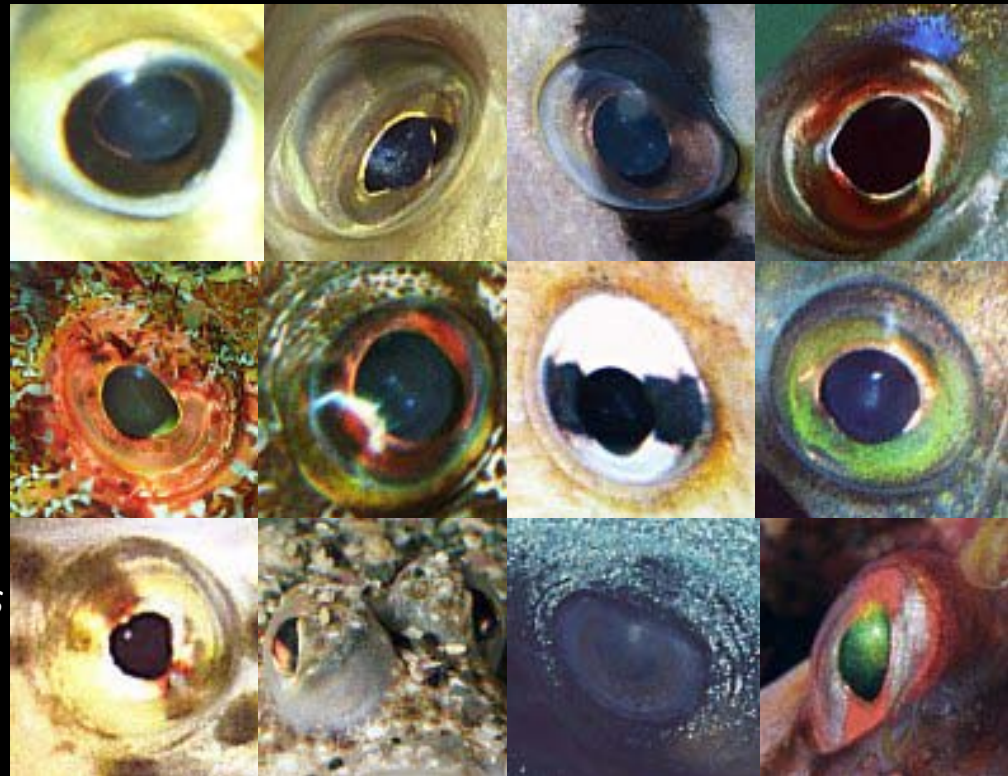
Retina

Function of the eye

Collection of light,

Focusing light

Conversion of light into neural impulses



Retinal structure and function

Pigmented epithelium

Photoreceptors

Bipolar and ganglion cells

Luminescence and vision

Adaptations to particular photoenvironments

Visual pigments

Changes in eye anatomy in migratory species

Deep sea vision

Amphibious vision



Introduction

Seeing under water and the diversity of fish habitats has shaped NUMEROUS VARIATIONS in the ANATOMY AND FUNCTION of fish eyes

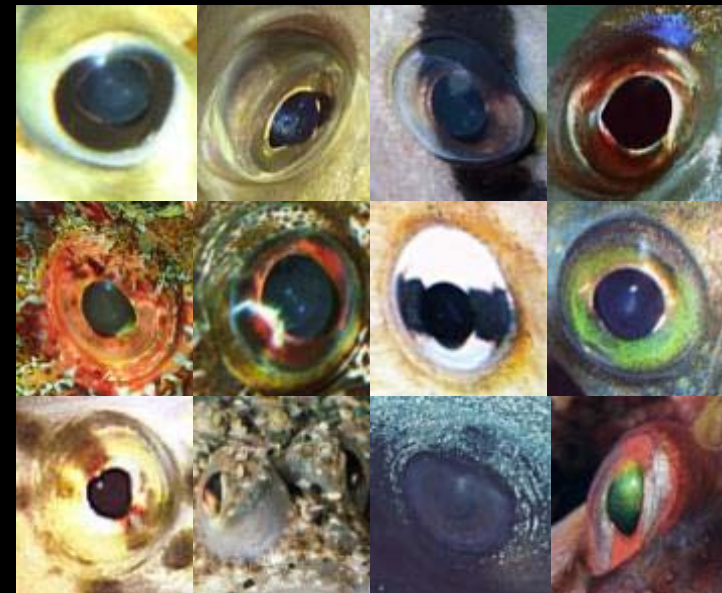
In addition to these functional differences, the FISH EYE CONTINUES TO GROW THROUGHOUT LIFE, it changes and ADDS NEW CELLS CONTINUOUSLY

However, fish eyes are similar to all other eyes in terms of THREE MAIN FUNCTIONS:

COLLECTING light

FOCUSSING images on the retina (accommodation)

TRANSFORMING images into neural signals



Optical properties of water

In order to understand the design and behavior of the normal eye it is necessary to understand its basic optical properties

Reflection, refraction and absorption

- Light is FILTERED BY THE ATMOSPHERE before it enters the water column
- At the water's surface, PHOTONS will be REFRACTED, REFLECTED and POLARISED
- Changes in the lighting characteristics are due to the DIFFERENTIAL ABSORPTION OR REFLECTION OF PHOTONS of different wavelengths
- Water also ABSORBS DIFFERENT COLOURS SELECTIVELY. First the reds and oranges disappear, later the yellows, greens and purples and last the blue
- In the DEEP OCEAN, the wavelength of light that is absorbed best is 470-480nm, 500-530nm in coastal water, and 550-560nm or longer in fresh water



Snell's law and Snell's window

When a light ray ENTERS WATER it is refracted (bent). The equation that describes this bending is known as SNELL'S LAW

$$\frac{\sin \theta}{\sin \theta'} = \frac{n_2}{n_1}$$

If water has an index of refraction of 1.33, then to calculate θ' then

$$n_1 \sin \theta = n_2 \sin \theta'$$

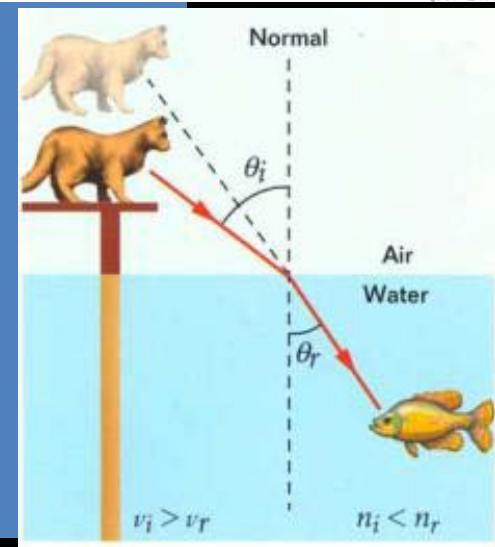
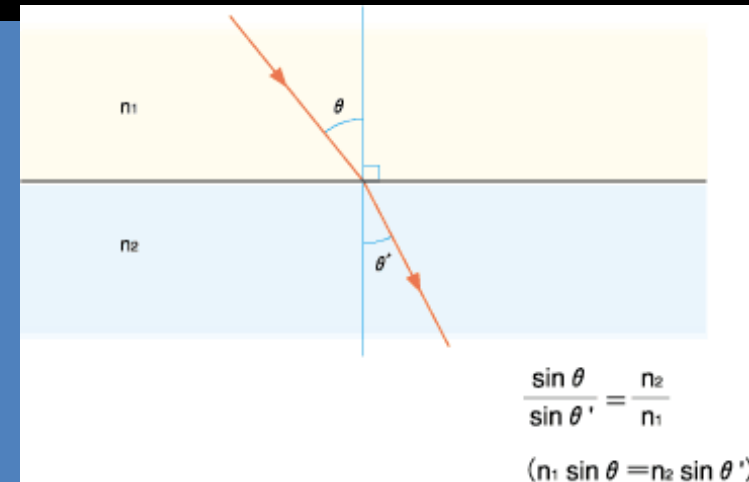
$$\sin \theta' = \frac{n_1 \sin \theta}{n_2}$$

$$\sin \theta' = \frac{1}{1.33}$$

$$\arcsin \theta' = 0.750188$$

$$\theta' = 0.848$$

In degrees $\theta' = 0.848 * 180 / \pi = 48.6$ and doubled = 97.2°



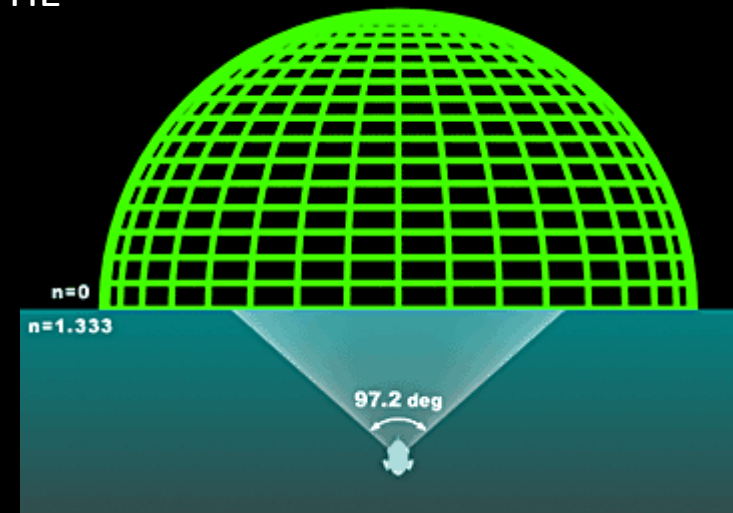
SNELL'S WINDOW is the phenomenon of **LIGHT REFRACTION THROUGH WATER**

Light that **ENTERS THE WATER** from horizon to horizon (180 degrees) is **REFRACTED INTO A CONE** approximately 97 degrees wide

The window's 97-degree angle is constant, with only the diameter of the window changing with depth (as the diameter is 2.26 times the depth)

The **LOWER THE ANGLE OF THE LIGHT** in relation to the water's surface **THE MORE IT IS REFRACTED** upon entering the water

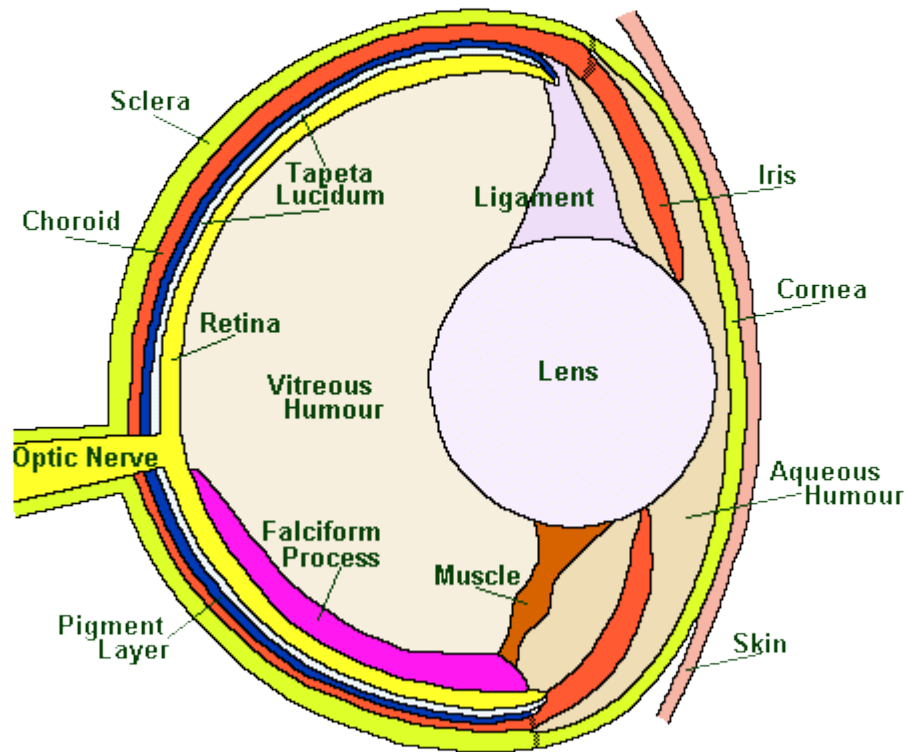
From below the surface of the water, the **WINDOW APPEARS AS A CIRCLE OVERHEAD**. The images **IN THE CENTER OF THE WINDOW** are **NORMAL IN SHAPE** and those images **NEAR THE FRINGES OF THE WINDOW** appear **DISTORTED**



Anatomy of the eye

Although fish eyes can vary significantly in their structure, generally they are HEMISPHERIC WITH A SHORT AXIAL LENGTH and consist of a CORNEA, IRIS, LENS, SCLERA, CHOROID.

A Diagrammatic Representation of a Teleost Eye

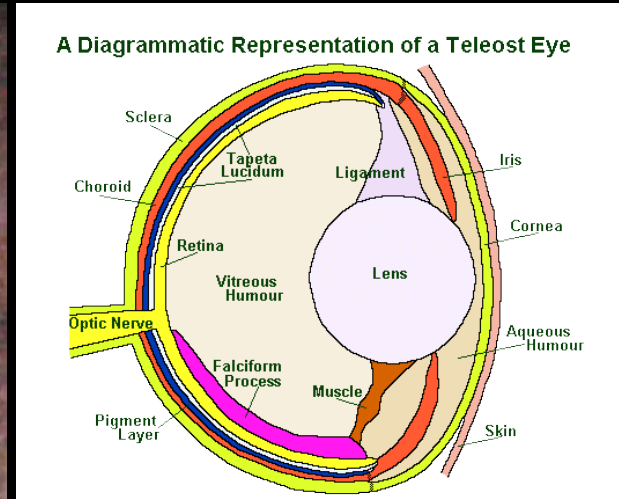


CORNEA

- OUTERMOST TRANSPARENT LAYER OF THE EYE
- Consists of CONJUNCTIVA and SCLERA
- FISH CORNEA IS THINNER than that of terrestrial vertebrates
- The optical properties of the water and the liquid inside the eye are similar = LITTLE REFRACTION

IRIS

- CONTROLS THE AMOUNT OF LIGHT ENTERING THE EYE by adjusting the diameter of the PUPIL
- ELASMOBRANCHS are able to ADJUST THE IRIS and change the shape of the pupil



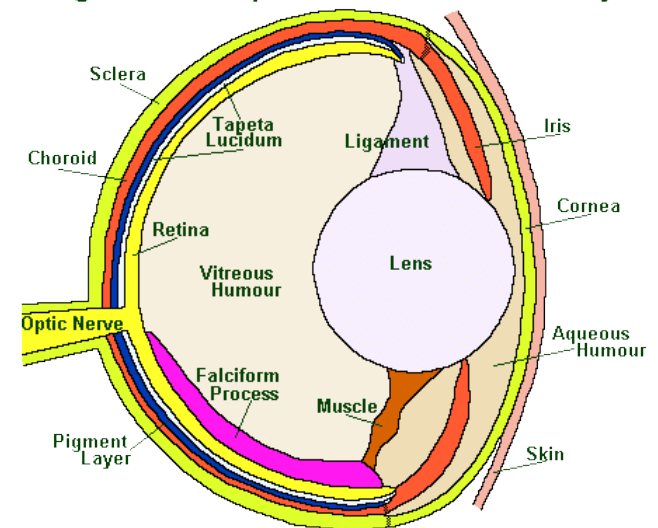
LENS

- FOCUSES LIGHT ON THE RETINA – adjustment of the lens is called ACCOMODATION
- BONY FISH and LAMPREYS have SPHERICAL LENSES and ELASMOBRANCH lenses are SLIGHTLY FLATTENED
- This differs from TERRESTRIAL VERTEBRATES have CONVEX LENSES.
- TERRESTRIAL ANIMALS focus by CHANGING THE CURVATURE of the lens
- FISH focus by moving the lens sideways by the RETRACTOR LENTIS muscle

SCLERA

- Forms the OUTER LAYER OF THE EYE and it protects the inner structures of the eye.
- AGNATHANS (hagfish and lampreys) = FIBROUS sclera
- CHONDRICHTHYANS (sharks, rays) = CARTILAGINOUS PLATES
- TELEOSTS (bony fish) = SCLEROTIC BONES (well-developed in the mackerels, tunas and billfishes)

A Diagrammatic Representation of a Teleost Eye



CHOROID

Highly VASCULARISED region BETWEEN THE SCLERA AND THE RETINA

The choroid MAY CONTAIN A TAPETUM LUCIDUM

This REFLECTS LIGHT passing through the retina BACK TO THE INNER LAYER of the retina.

Composed of REFLECTIVE GUANINE CRYSTALS that ENHANCES VISUAL SENSITIVITY in conditions when light intensity is low

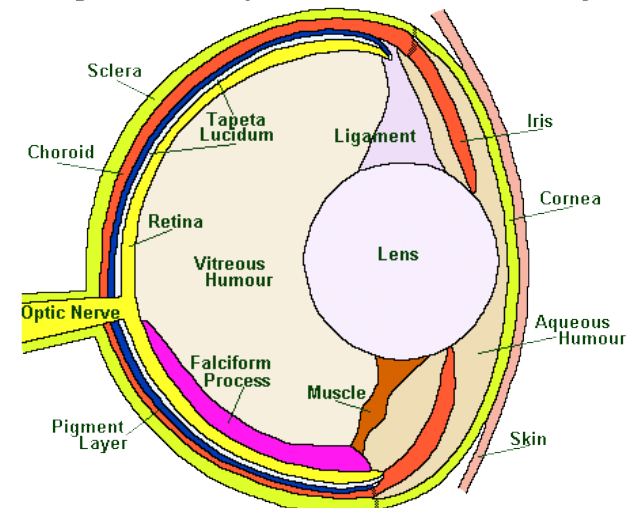
Found in most ELASMOBRANCHS, the HOLOCEPHALI, the COELACANTH, STURGEONS and SOME TELEOSTS

CAUSES REFLECTIVE SHINE in the eyes of most sharks and nocturnal fishes.

DISADVANTAGE = fish become conspicuous when illuminated by daylight. The TAPETUM IS CONCEALED by the migration of black masking pigment



A Diagrammatic Representation of a Teleost Eye



RETINA

A THIN, TRANSPARENT LAMINAR STRUCTURE situated at the back of the eye

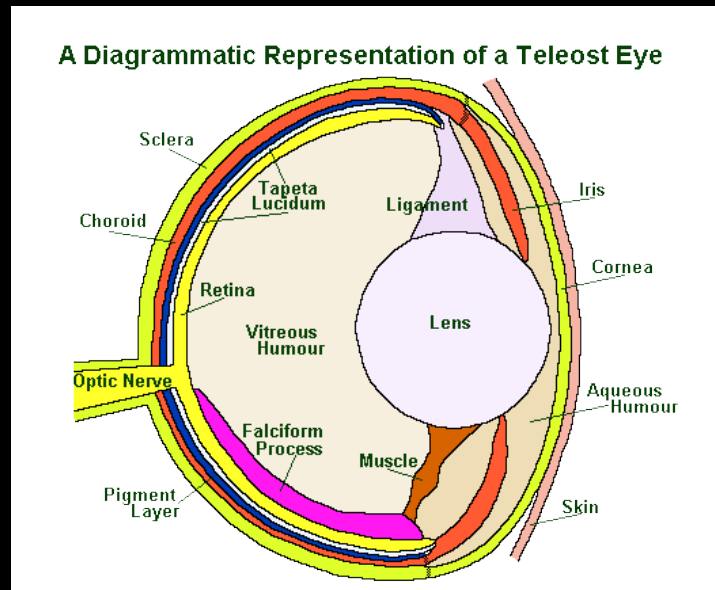
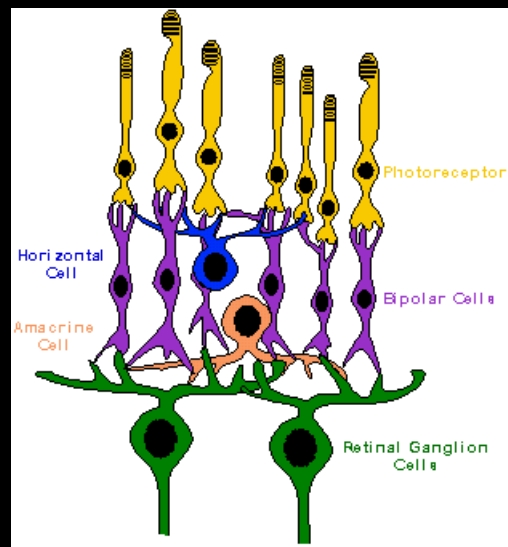
The retina is sandwiched BETWEEN the VITREOUS BODY of the actual eyeball, and the SCLERA

The retinas of fishes DO NOT DIFFER FUNDAMENTALLY FROM THOSE OF OTHER VERTEBRATES

They can be divided into 2 layers - the OUTER and INNER layers

The OUTER LAYER is made up of the PIGMENTED EPITHELIUM layer and the PHOTORECEPTORS

The INNER LAYER is made up of NERVOUS TISSUE and has NUCLEI OF THE PHOTORECEPTORS, BIPOLAR and GANGLION CELLS



They may differ significantly
depending on where and how they
live. Here is an example of a weird fish
eye!

http://www.liveleak.com/view?i=0d7_1276442602



Function of the eye

To see the eye must do three things:

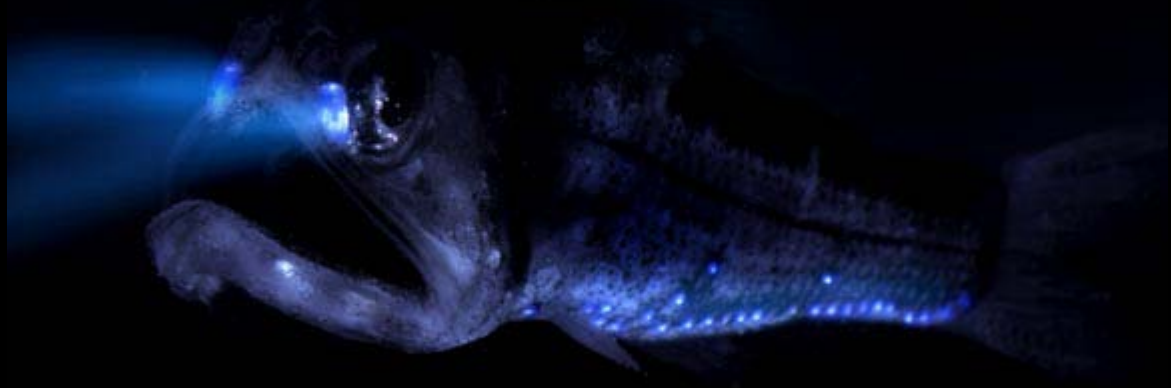
1. collect light,
2. Focus light onto the retina
3. Convert the light into neural impulses

Collection of light

The CLARITY OF AN IMAGE on the retina DEPENDS ON ITS BRIGHTNESS

BRIGHTNESS is increased BY THE AREA OF THE PUPIL and the INTENSITY OF THE LIGHT SOURCE

Where there is no light, deep sea fishes often use bioluminescence to light up the area around the eye.



Focus of light

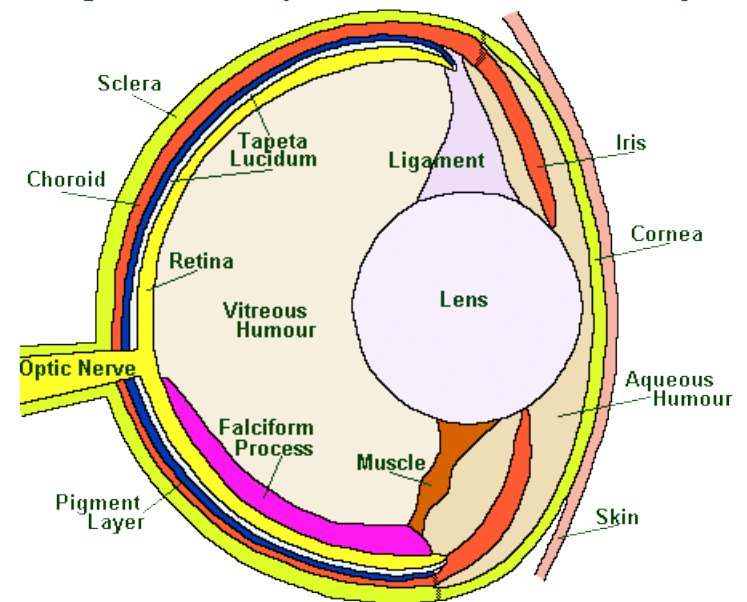
The CORNEA HAS LITTLE INFLUENCE ON THE REFRACTION of light through the eye. All focusing is therefore done by the lens

Fish focus their eyes via RETRACTOR LENTIS muscles

This muscle pulls the lens backwards. The ANTERIOR PORTION OF THE LENS is attached to the cornea via a SUSPENSORY LIGAMENT. RELAXATION OF THE MUSCLE will allow the lens to RESUME ITS POSITION

AT RESTING THE FISH IS A LITTLE SHORT SIGHTED

A Diagrammatic Representation of a Teleost Eye



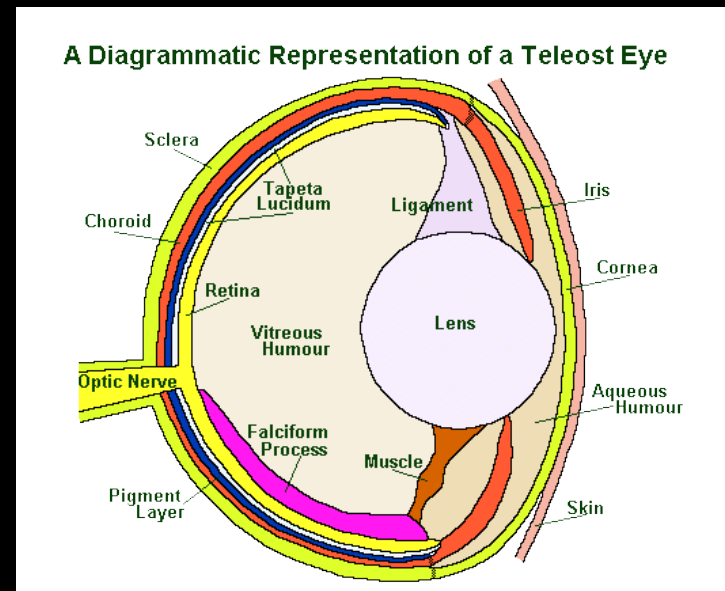
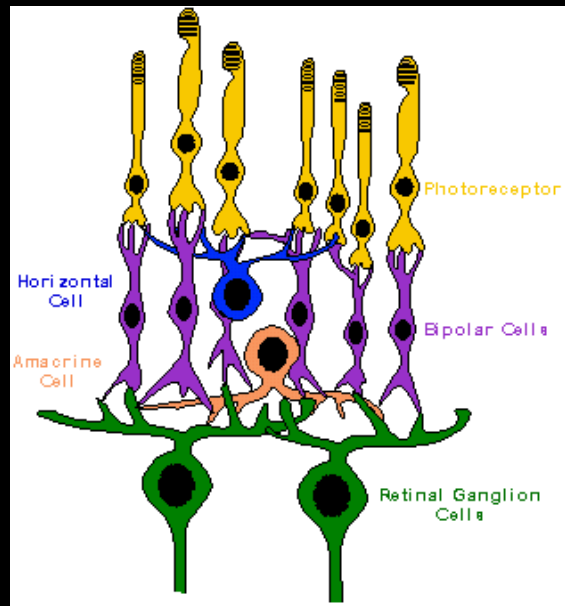
Conversion into neural impulses

VISUAL INFORMATION ARRIVES AS PHOTONS

Photons travel through the lens and are ACCOMMODATED ON THE RETINA

These photons are then TRANSLATED INTO NEURAL IMPULSES via specialized cells in the retina, the RODS, CONES, BIPOLAR CELLS and GANGLION CELLS

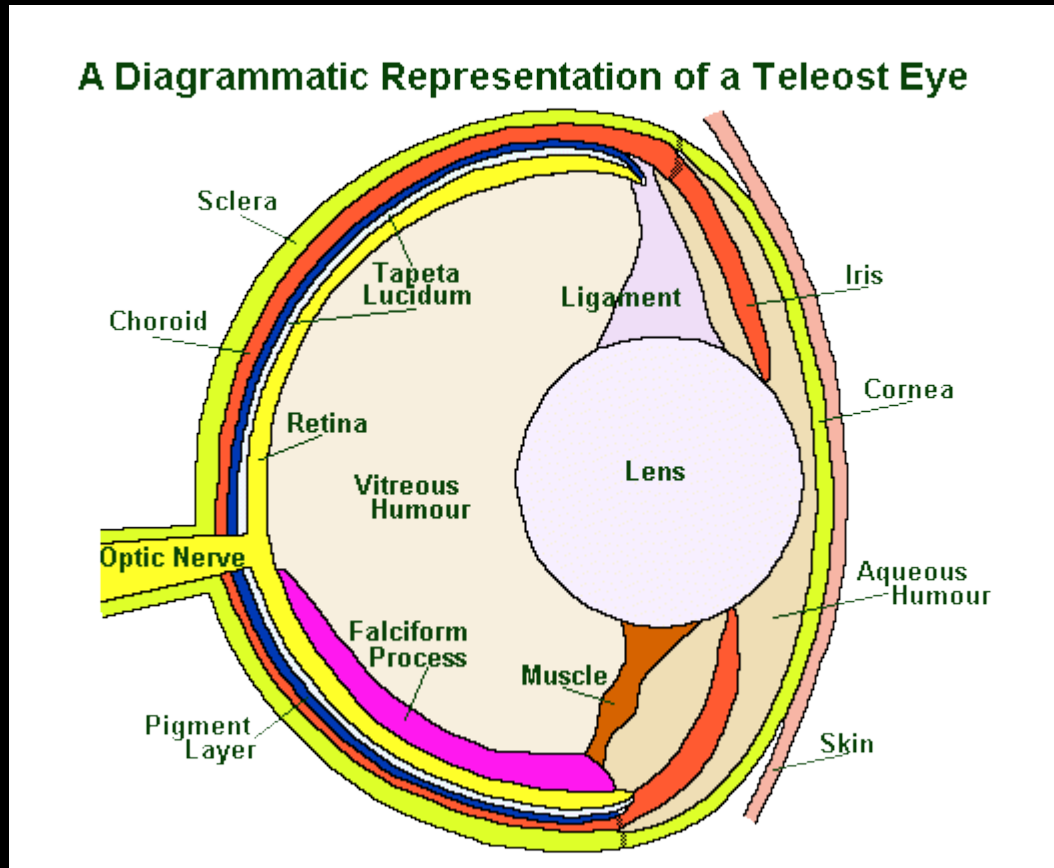
The GANGLION CELLS then TRANSMIT THESE IMPULSES TO THE BRAIN via THE OPTIC NERVE



- End lecture 1

Anatomy of the eye

Although fish eyes can vary significantly in their structure, generally they are HEMISPHERIC WITH A SHORT AXIAL LENGTH and consist of a CORNEA, IRIS, LENS, SCLERA, CHOROID and RETINA.



Photoreceptors

Fishes have a DUPLEX RETINA – meaning they have RODS AND CONES

Some HOLOCEPHALANS and ELASMOBRANCHS only RODS as do deep-sea fishes.



In LARVAL FISHES, CONES DEVELOP FIRST and then rods develop



CONES are generally found in DIURNALY ACTIVE SPECIES and RODS in NOCTURNALLY ACTIVE SPECIES

ROD and CONE structure

Rods and cones have a similar basic structure:

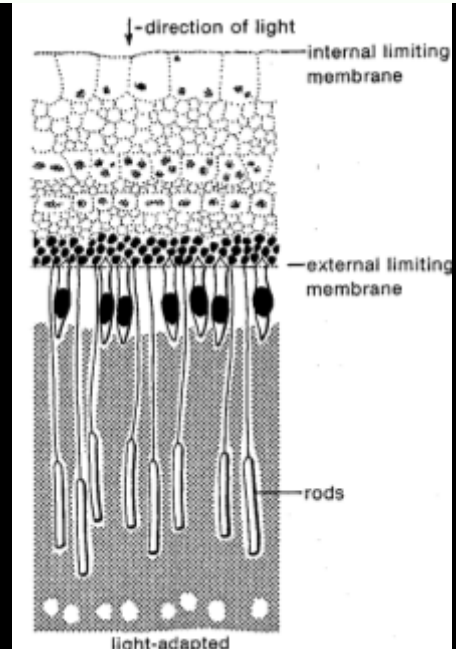
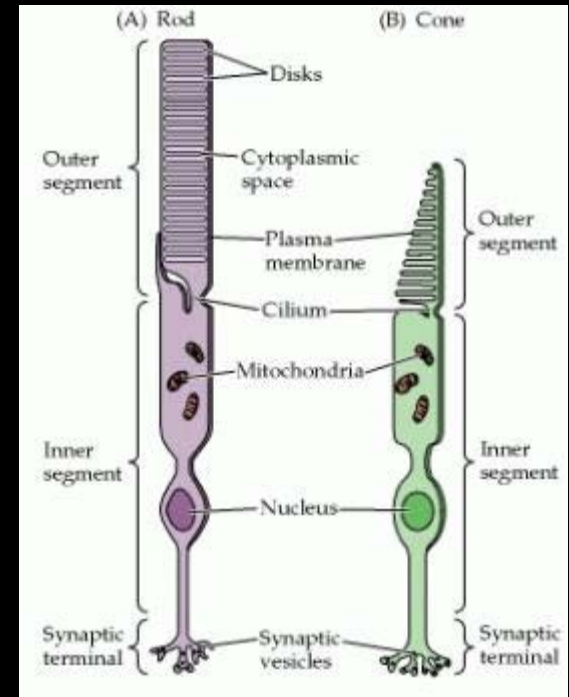
They have an OUTER SEGMENT that contains the VISUAL OR PHOTSENSITIVE PIGMENT an ELLIPSOID, which is packed with MITOCHONDRIA, an EXTENSIBLE MYOID or foot-piece, and a NUCLEAR REGION.

The rods and cones are HELD IN PLACE BY AN EXTERNAL LIMITING MEMBRANE.

RODS ARE LONGER AND THINNER with CYLINDRICAL OUTER SEGMENTS and ELLIPSOIDS

CONES have a CYLINDRICAL OUTER SEGMENT but a BULBOUS ELLIPSOID

Retinal area of specialization = AREA TEMPORALIS = CLOSELY PACKED CONES



Retinal structure and function

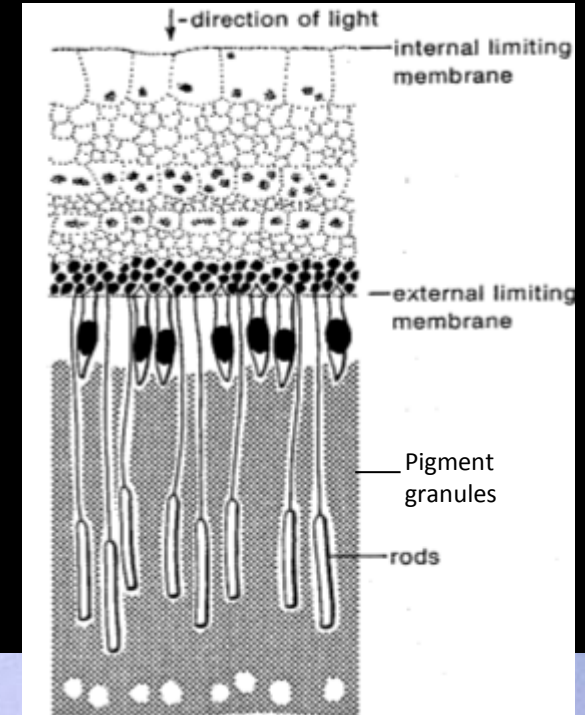
Pigmented epithelium

This epithelium is made up of a LAYER OF CUBOIDAL CELLS which is situated on the OUTER LAYER OF THE RETINA

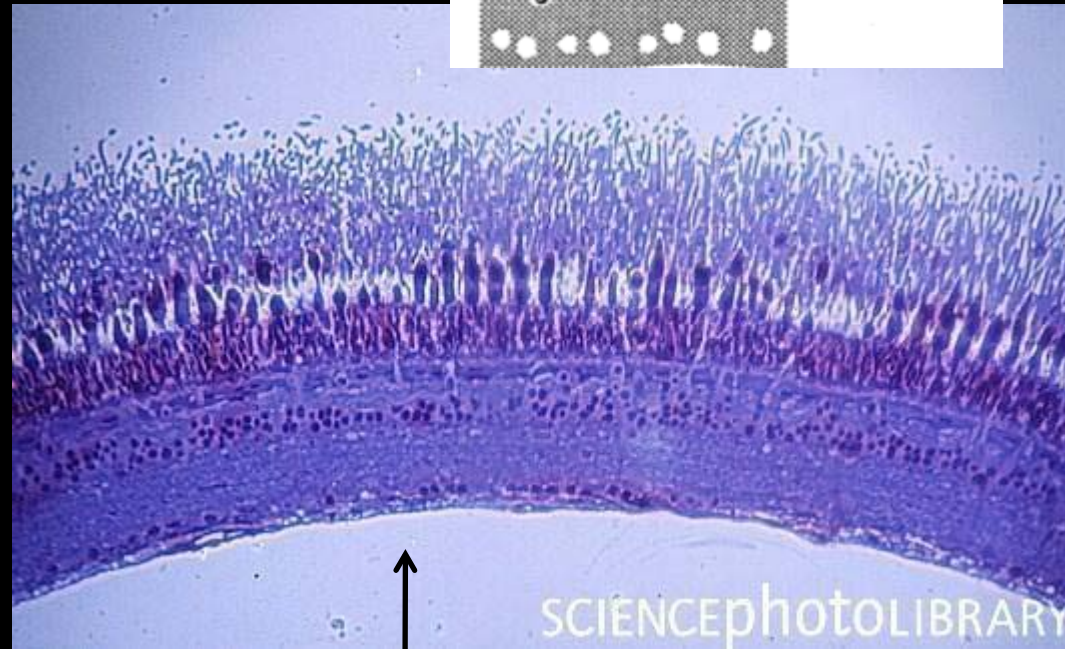
On the INNER SIDE OF THE EPITHELIUM, it has LONG PROCESSES that extend into the retinal cells, SURROUNDING THE TIPS OF THE PHOTORECEPTORS

WITHIN THE CELLS are ROD-SHAPED PIGMENT GRANULES that absorb light

During BRIGHT ILLUMINATION, these GRANULES ISOLATE THE CONE, OUTER SEGMENTS, and PROTECT THE ROD- OUTER SEGMENTS



Caption: Light micrograph of the retina from a freshwater roach, *Rutilus rutilus*. The top of the photo shows the rods (thin) & cones (bulbous/purple), the light sensitive cells of the retina. The band forming an arc of dense cells (bottom) is the pigment layer, beneath which is the choroid containing blood vessels. The cones are the receptors responsible for daylight & colour vision. Rods are responsible for night or "dark" vision. The rest of the retina (not visible) consists of layers of functionally different nerve cells. They transmit visual information as electrical signals to the ganglion nerve, which is connected to the brain. Mag: X63 (at 35mm size).



The RODS DO RESPOND TO DIM LIGHT but with POOR ACUITY OR SHARPNESS and without colour perception

CONES are DIVIDED INTO POPULATIONS, and EACH POPULATION HAS A DIFFERENT VISUAL PIGMENT

TELEOSTS are able to ADAPT their eyes to bright and dim light

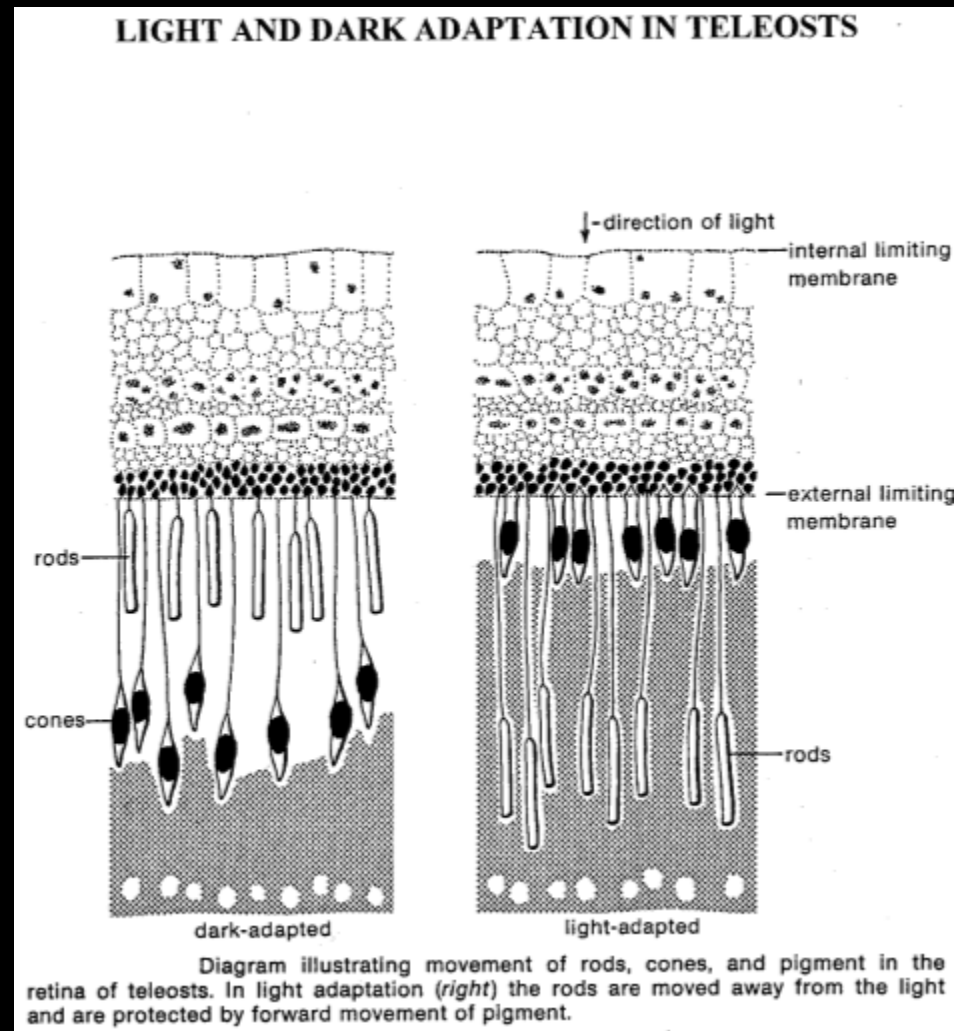
This LIGHT AND DARK ADAPTATION is accompanied by the MOVEMENT OF THE VISUAL CELLS and the PIGMENT GRANULES

In DIM LIGHT, the PIGMENT GRANULES are PULLED BACK towards the outside of the retina

The ROD MYOIDS are SHORT and the CONE MYOIDS LONG

As the EYE ADAPTS TO LIGHT, the CONE MYOIDS SHORTEN bringing their OUTER SEGMENTS CLOSER TO THE EXTERNAL LIMITING MEMBRANE

At the same time, the ROD MYOIDS LENGTHEN, and the OUTER SEGMENTS BECOME SURROUNDED BY THE PIGMENT GRANULES which protect them against the bright light



The RODS AND CONES are
CONNECTED to the brain via the
BIPOLAR AND GANGLION CELLS,
which maybe connecte laterally by
AMACRINE CELLS

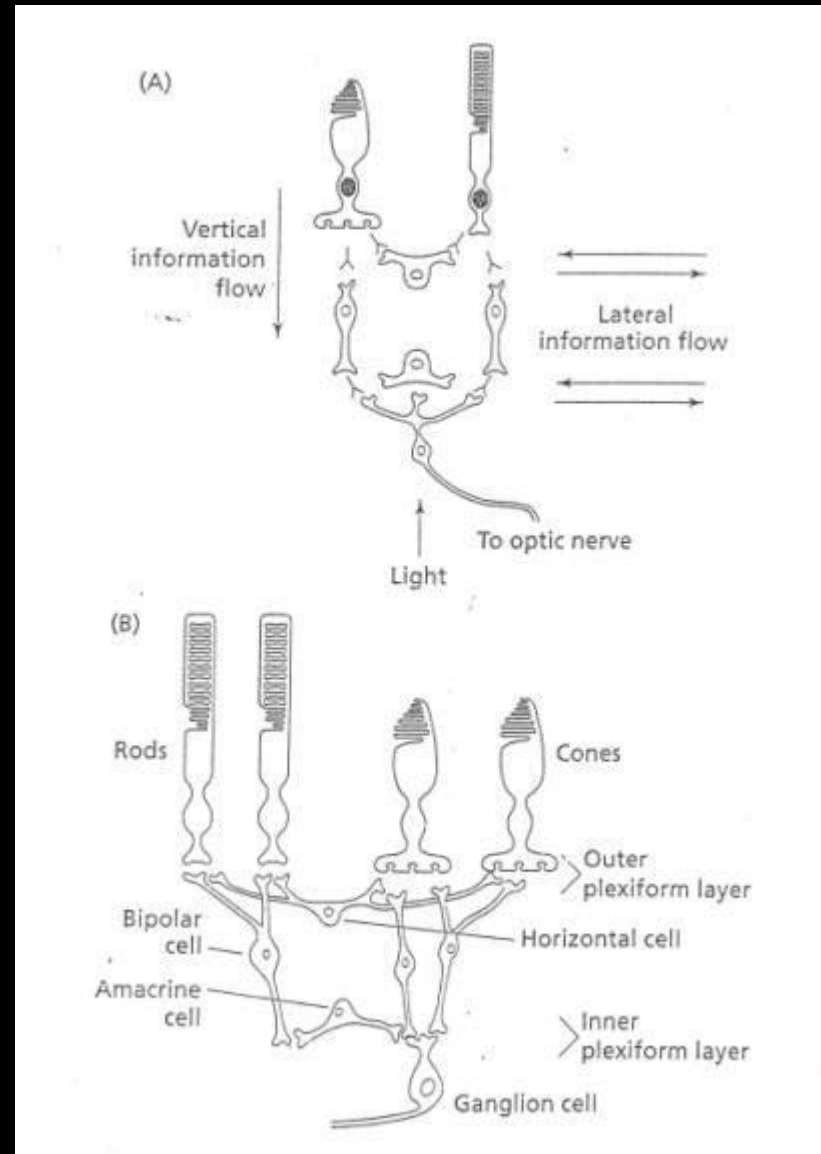
The AXONS (slender projection of the
neuron) OF THESE CELLS pass
along the OPTIC NERVE to the
OPTIC LOBE

The RODS contain MORE VISUAL
PIGMENT THAN CONES, and are
therefore MORE SENSITIVE

The SENSITIVITY OF THE RODS IS
ENHANCED by the CONVERGENCE
of many rods to one bipolar cell =
SUMMATION

NO SUMMATION IN CONES

The COMBINED EFFECT of light on a
number of rods can be ADDITIVE
and assists in firing the bipolar cell

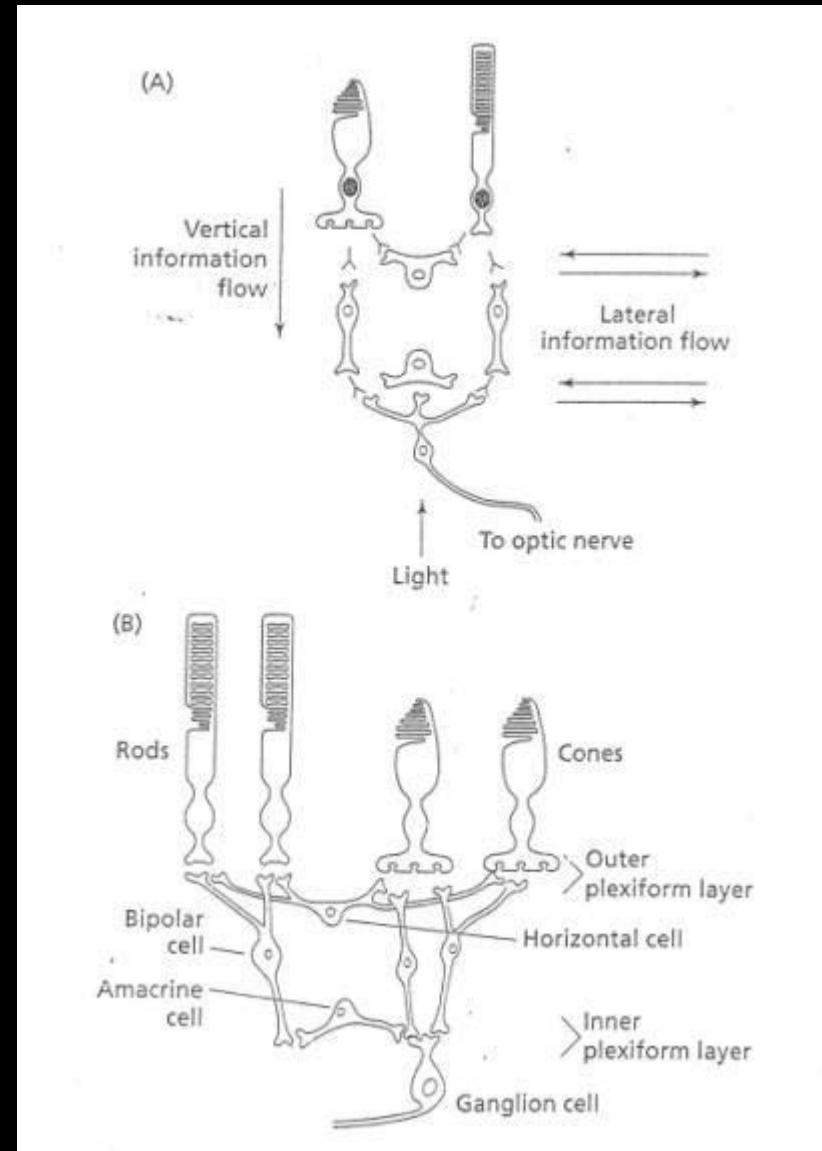


Information flow via rods, cones, bipolar cells and ganglion cells

Bipolar and ganglion cells structure

INFORMATION FROM THE RODS AND CONES is passed on to the brain VIA THE BIPOLAR AND GANGLION CELLS.

BIPOLAR CELLS can be divided into MIXED BIPOLAR CELLS (connected to rods and cones), PURE CONE BIPOLAR CELLS (connected only to cones) and PURE ROD BIPOLAR CELLS (connected only to rod)



Information flow via rods, cones, bipolar cells and ganglion cells

Bipolar and ganglion cells function

Functionally, BIPOLAR CELLS can be classified as ON- OR OFF-CELLS.

When ON

The BIPOLARS release EXCITATORY NEUROTRANSMITTERS during light stimulus.

When OFF-

The BIPOLARS release EXCITATORY NEUROTRANSMITTERS in the dark and immediately after the termination of a light stimulus.

The ON-BIPOLAR cells connect with ON-GANGLION CELLS and visa versa

The ON-CELLS DEPOLARISE to a light stimulus while the OFF-CELLS HYPERPOLARIZE

The STIMULI ARE THEN PASSED ON TO THE OPTIC NERVE and finally TO THE BRAIN

Luminescence and vision

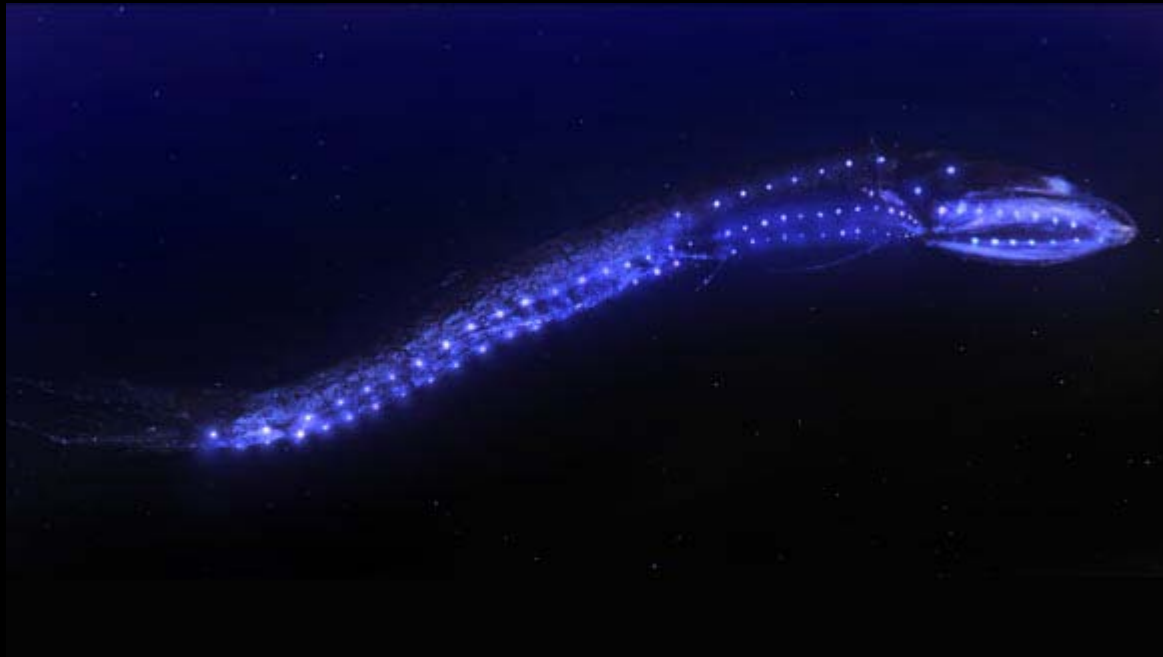
BIOLUMINESCENCE is the LIGHT PRODUCED BY BACTERIA usually in special organs in fishes.

About HALF OF THE SPECIES OF DEEP-SEA FISHES living below 1000m are luminescent

The VISUAL MECHANISMS of fishes in the mesopelagic zone must be ADAPTED to luminescence as well as to residual natural light

MANY FISHES in this zone MIGRATE TOWARDS THE SURFACE AT NIGHT and continue to utilise luminescence

This LIGHT IS WEAK and the SOURCES SMALL so a HIGH SENSITIVITY is required to make use of it

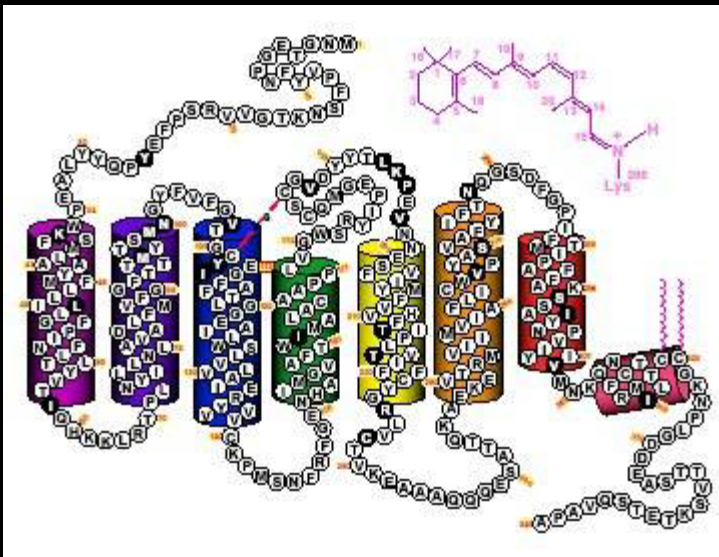


Adaptations to particular photoenvironments

Visual pigments

RHODOPSINS and PORPHYROPSINS (made up of a protein called opsin linked to an aldehyde of vitamin A1 or A2) are the DOMINANT VISUAL PIGMENTS

These PIGMENTS ABSORB LIGHT OF DIFFERENT WAVELENGTHS and generally MATCH THE SPECTRUM CHARACTERISTICS to the photo-environment in which the fish lives



Changes in eye anatomy in migratory species

The difference in habitat necessitates change in visual pigments.

Lampreys

Migrate from fresh to salt water, therefore, different visual pigments for each habitat

PORPHYROPSIN in FRESH WATER (red light)

RHODOPSIN in the OCEANIC WATER (blue light)



Changes in eye anatomy in migratory species

The difference in habitat necessitates change in visual pigments.

Eels

In FRESH WATER = retina is PACKED WITH RODS (cones = 3% of the photoreceptors)

Prior to downstream migration to the sea

DIAMETER OF THE EYE INCREASES by more than double = fourfold increase of the retinal surface and a 8-fold increase in volume.

LENS ENLARGES

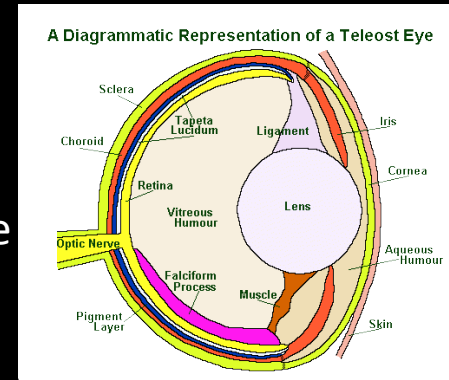
NUMBER OF RODS INCREASES although their density remains constant.

THE CONES DECREASES in density as the retinal area increases

GANGLION CELLS DECREASE in number

leads to a CONVERGENCE OF THE RODS AND INCREASES IN VISUAL SENSITIVITY but a decreased

DENSITY OF VISUAL PIGMENT in the retina INCREASES and dominated by rhodopsins



Amphibious vision

Flying fish

CORNEA IS MODIFIED into a low, 3-SIDED PYRAMID with slightly bulging sides

The fish LOOKS UP AND FORWARD THROUGH THE ANTERIOR SURFACE of the pyramid, UP AND BACKWARD THROUGH POSTERIOR SURFACE, and DOWN THROUGH THE VENTRAL SURFACE

In AIR the fish has 'normal' vision, but UNDERWATER it is FAR SIGHTED



Amphibious vision

The four-eyed fish *Anableps* swims just below the water surface

- They have LARGE, PROTUBERANT EYES that are DIVIDED BY THE WATER MENISCUS. So, the UPPER HALF IS IN AIR and the LOWER HALF IN WATER
- At the level of the eye that corresponds with the water level, there is a HORIZONTAL BAND OF PIGMENT IN THE CORNEA
- ABOVE this band, the CORNEA IS THICK and THIN BELOW
- The fish also has two horizontal IRIS FLAPS that cross at water level
- WHEN the eye has ADAPTED TO DARK CONDITIONS the pupil has an hourglass shape with a LARGE UPPER APERTURE
- When the eye is ADAPTED TO LIGHT the horizontal IRIS FLAPS OVERLAP forming two SEPARATE PUPILLARY APERTURES
- The DORSAL RETINA receives images from the LOWER AQUATIC FIELD while the VENTRAL RETINA receives images from the AERIAL FIELD

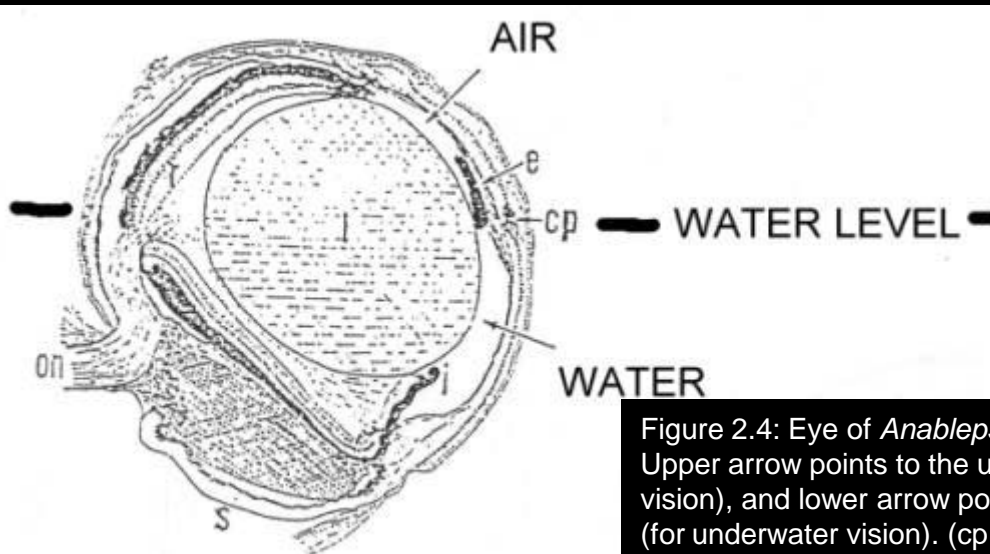
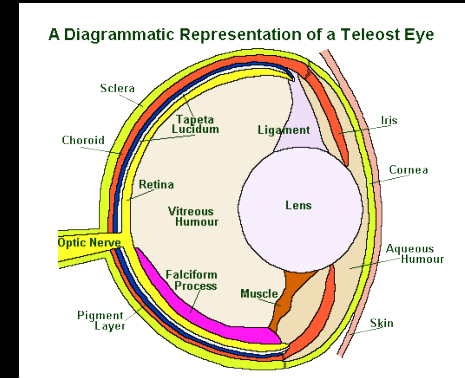
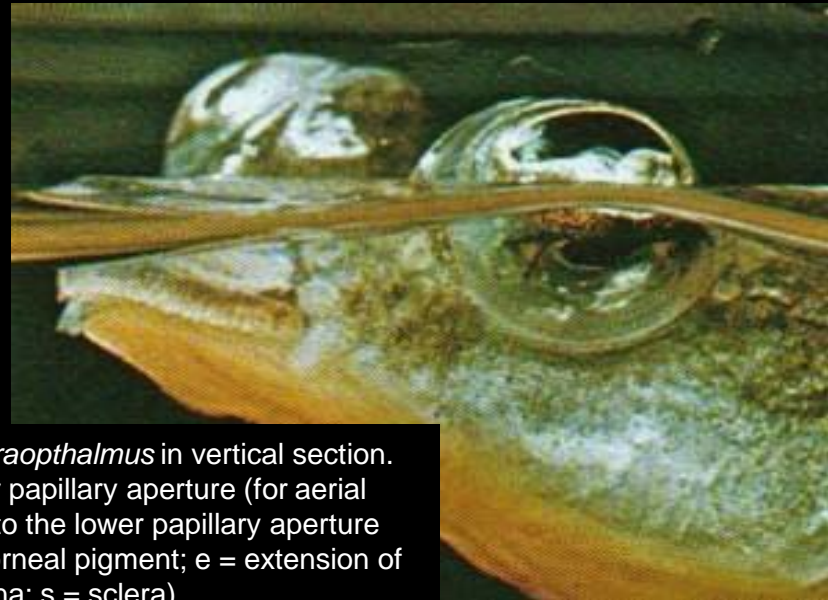


Figure 2.4: Eye of *Anableps tetraopthalmus* in vertical section. Upper arrow points to the upper papillary aperture (for aerial vision), and lower arrow points to the lower papillary aperture (for underwater vision). (cp = corneal pigment; e = extension of the iris; on = optic nerve; r = retina; s = sclera)



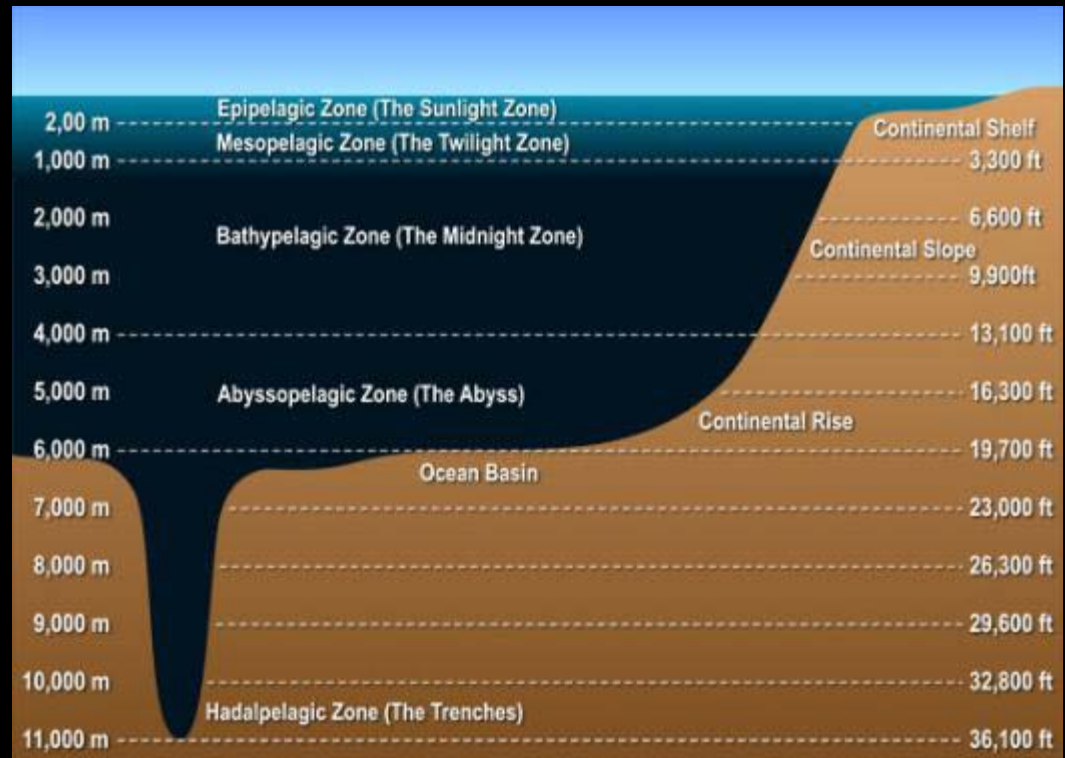
Deep-sea vision

The amount of light filtering into the sea decreases with an increase in depth.

The EPIPELAGIC REGION is WELL-LIT

The MESOPELAGIC REGION (200 and 1000m) forms a TWILIGHT REGION

Below 1000m in the BATHYPELAGIC REGION there is NO light. Lit only by LUMINESCENCE



Deep-sea vision

Eye size

MESOPELAGIC FISHES generally have LARGE EYES with WIDE PUPILS and ENLARGED LENSES

Some fishes have specially modified eyes, called TUBULAR EYES, such as the telescope fish.

BATHYPELAGIC FISHES TEND TO HAVE SMALL OR DEGENERATE EYES such as the ceratiid anglerfishes and the gulper eels.

These eyes generally have DISPROPORTIONATELY LARGE LENSES that are incapable of producing a clear images on the retina

The RESOLVING POWER IS LOW and the fishes can only detect objects close to them



Deep-sea vision

Tubular eyes

Some meso- and bathypelagic fishes have large eyes with a tubular or cylindrical shape

These include the free-living metamorphosed anglerfishes

These EYES POINT FORWARDS OR UPWARDS.

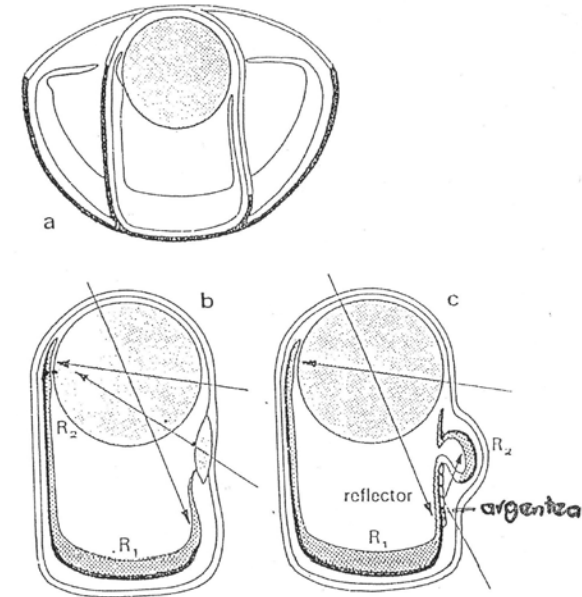
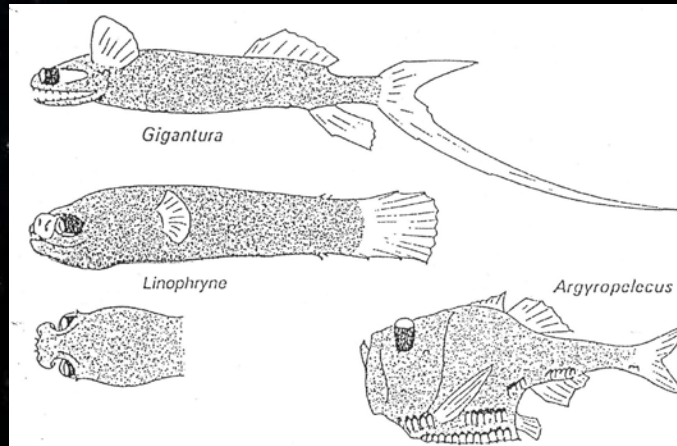
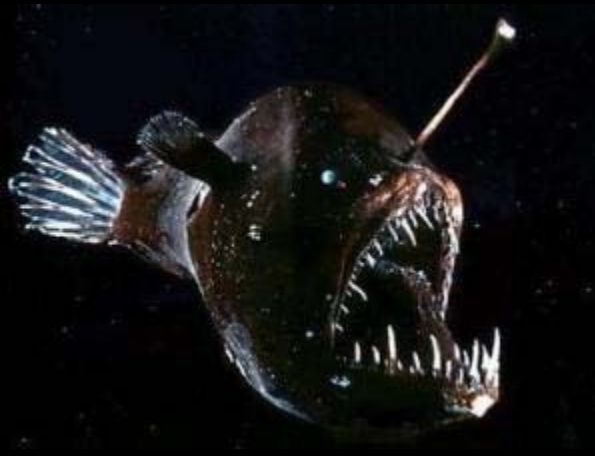


Figure 2.5: Mesopelagic fish (left) with tubular eyes. *Lynophryne* looks through its transparent olfactory organ. Right – modifications for lateral vision. A) tubular eye of *Argyropelecus* superimposed on a normal fish eye. B) *Scopelarchus* showing accessory scleroid lens. C) *Dolichopteryx* with reflector and accessory globe. (R_1 and R_2 are the main and accessory retinae, respectively)

Advantage and disadvantages of tubular eyes

ADVANTAGES:

- GOOD BINOCULAR VISION in one direction
- LARGE LENS WITH GOOD LIGHTING PROPERTIES without taking up too much space
- can LOOK PREDOMINANTLY UPWARDS to see their prey in silhouette against the vertically downwelling light

DISADVANTAGES:

- The PERIPHERAL PARTS of the retina CANNOT BE BROUGHT INTO FOCUS as they are too close to the lens . In these cases, these parts of the eye are probably ONLY USED FOR UNFOCUSSED MOVEMENT DETECTION

Example:

Some species have developed an ACCESSORY RETINA or ACCESSORY REFRACTING DEVICES

Scopelarchus has an ACCESSORY RETINA that is ILLUMINATED BY LATERAL LIGHT

This LIGHT DOES NOT PASS THROUGH THE LENS but through the side of the eye

On the side of the eye is a REFLECTOR CALLED THE ARGENTEA

Light falling onto, it is then REFLECTED ONTO THE ACCESSORY RETINA allowing the fish to see images from an angle at which it would not have been able to see otherwise



- End of lecture