

# Chemoreception

Is the physiological response of a sense organ to a chemical stimulus

Outline:

**Introduction**

**Olfactory system**

*Peripheral olfactory system*

*Olfactory epithelium structure*

**Gustatory system**

*Taste buds*

*Cell contacts and nerves*

**Signal transduction in olfaction and gestation**

**Chemoreception and fish behaviour**



# Chemoreception

Is the physiological response of a sense organ to a chemical stimulus. It plays a major role in the lives of fishes, including feeding, prey detection, predator avoidance, species and sex recognition, sexual behaviour and migration.

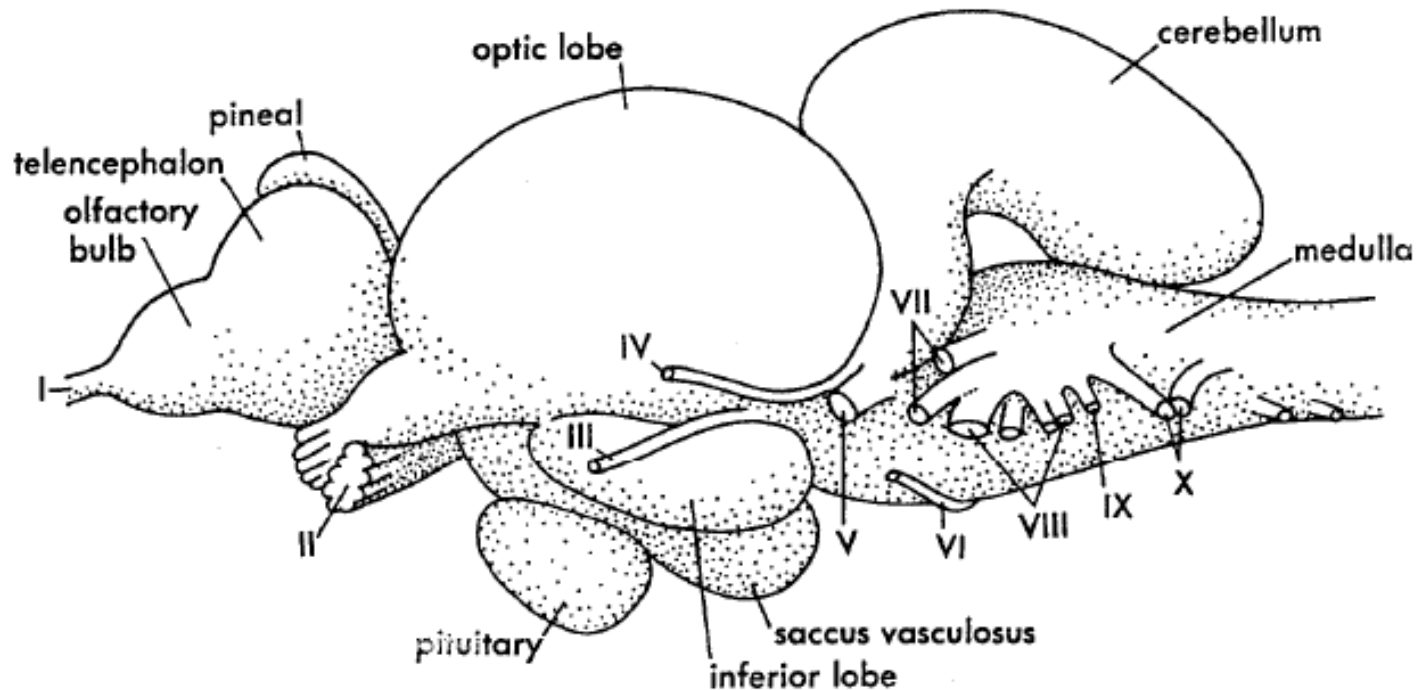
Fish detect chemical stimuli through TWO MAJOR CHANNELS OF CHEMORECEPTION:

OLFACTION, or smell

GUSTATION, or taste

In the aquatic environment the DISTINCTION between these senses can become BLURRED

Olfaction (smell): results from stimulation of the sensory receptor cells in the olfactory organs, which are innervated by the OLFACTORY NERVE (cranial nerve I)

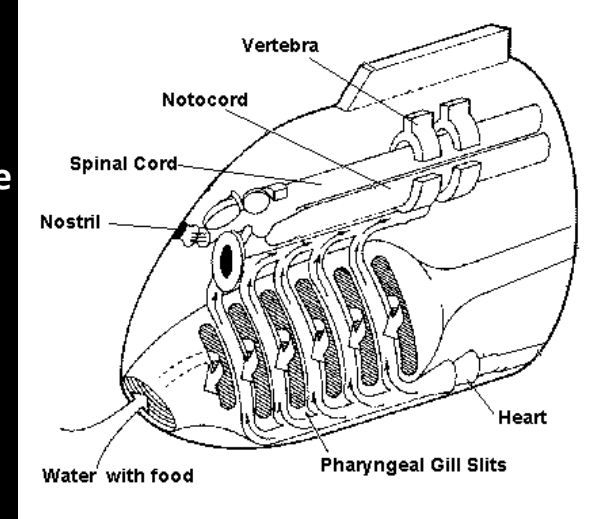


**Lateral view of the brain and roots of the cranial nerves of a salmon: olfactory nerve (I), optic nerve (II), oculomotor nerve (III), trochlear nerve (IV), trigeminal nerve (V), abducens nerve (VI), facial nerve (VII), auditory nerve (VIII), glossopharyngeal nerve (IX), and vagus nerve (X)**

# Olfactory system

## Peripheral olfactory system

- This receives the information from the environment and transports the information via nerves to the brain.
- The olfactory organs show considerable variation and generally reflects variability in development and ecological habitats

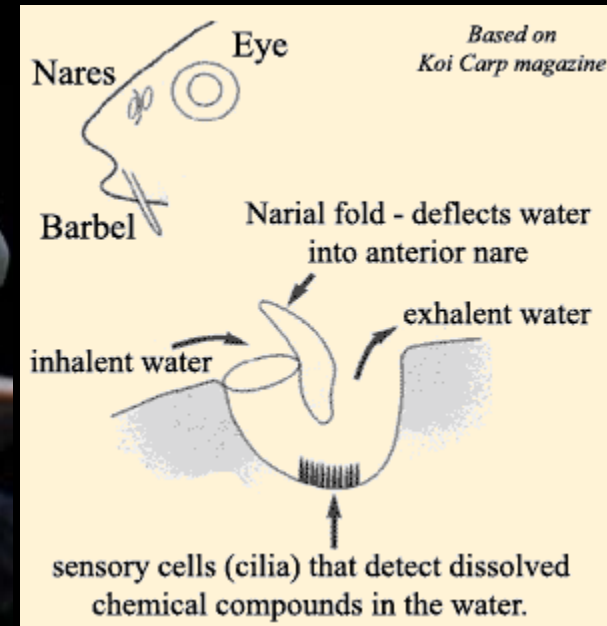


AGNATHANS - one olfactory organ with a single nostril

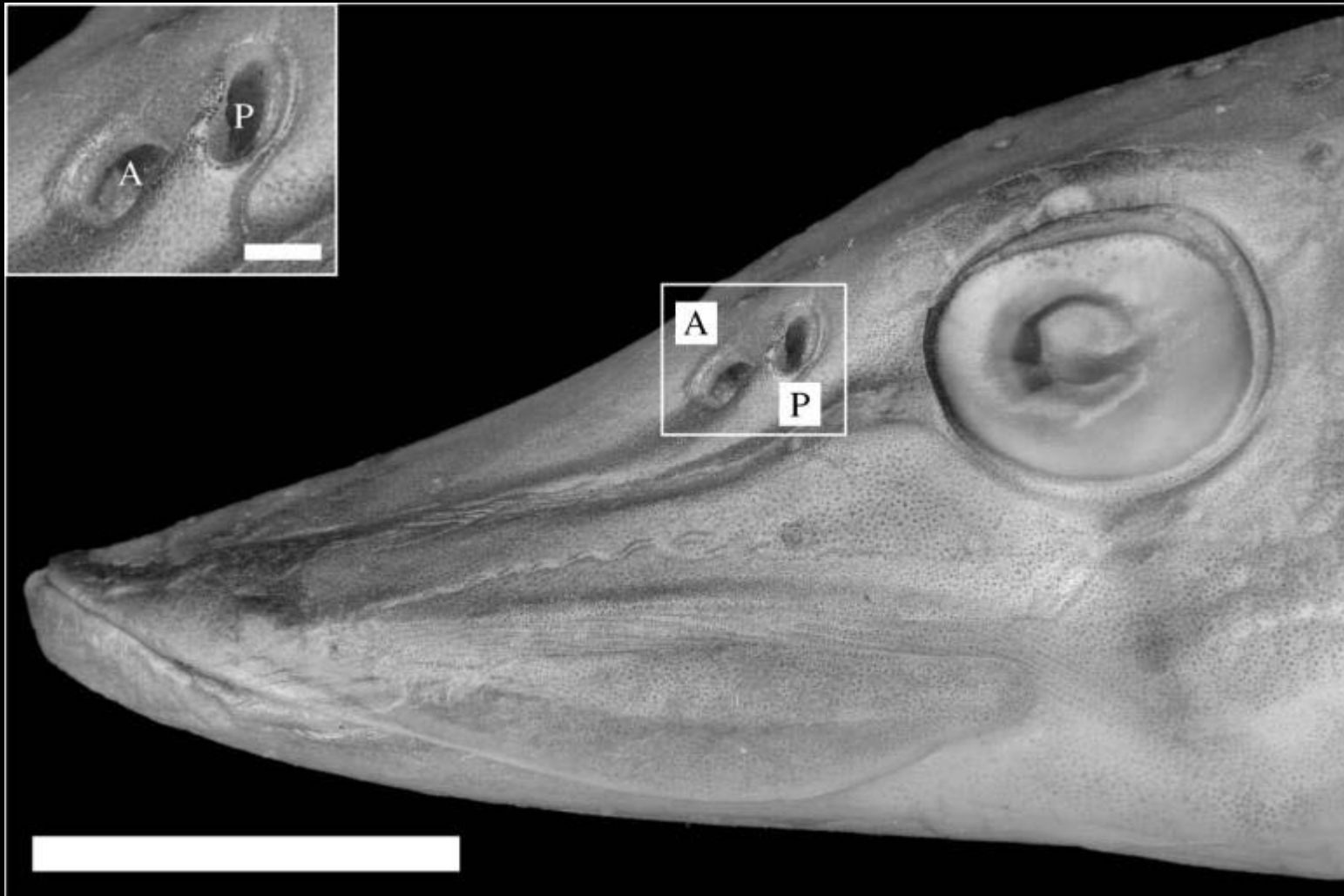
ELASMOBRANCHS - the paired olfactory pits or sacs are usually situated on the ventral side of the snout

TELEOST fishes - the paired olfactory organs are usually located on the dorsal side of the head

The opening of each nostril or nare is divided into 2 parts by a fold of skin. This forms an ANTERIOR INLET or naris, and a posterior outlet or naris. WATER ENTERS the ANTERIOR NARIS and LEAVES THROUGH THE POSTERIOR NARIS as the fish swims



Photograph of the head of a preserved northern pike (*Esox lucius*) specimen (total length 17cm), lateral (l.h.s.) aspect. Boxed region highlights the anterior (A) and posterior (P) nostrils. Scale bar, 1 cm.



Cox J P J. R. Soc. Interface 2008;5:575-593

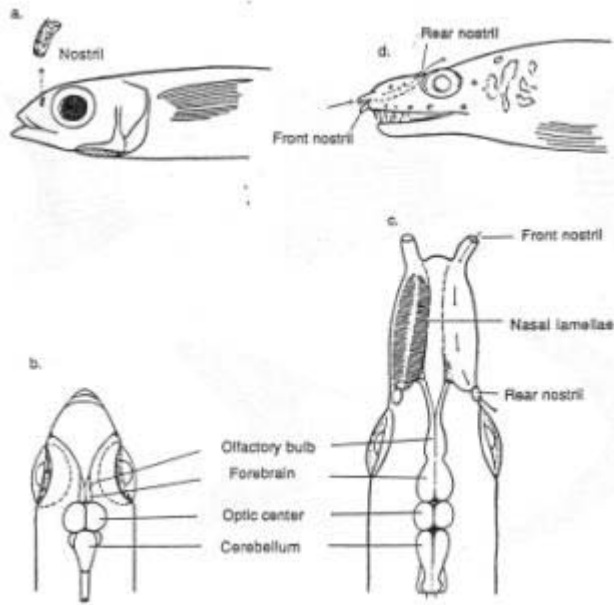


Figure 4.1: Diagrams of the olfactory organs and their relationship to the brain in two teleost fishes; a) side view and b) top view of the head of a flying fish with reduced development; c) top view and d) side view of the well-developed organs of a moray eel.

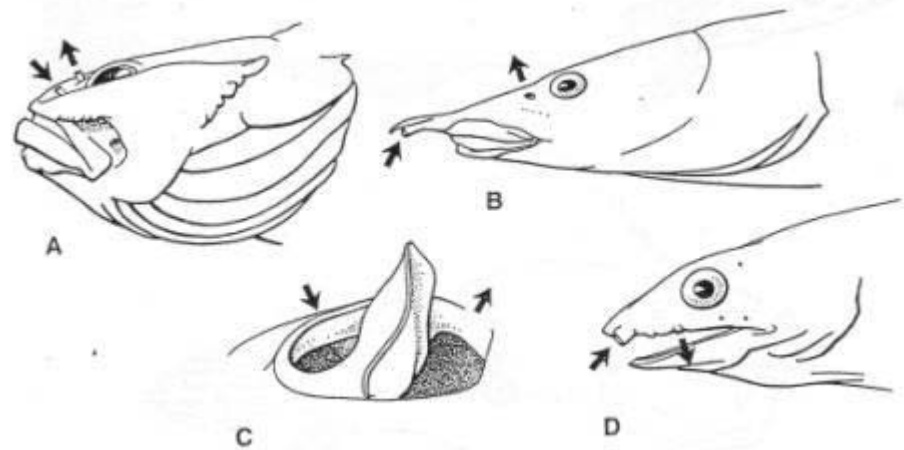


Figure 4.2: Nostril positions A) Sculpin, B) spiny eel and C) typical teleost nostrils divided by a flap of skin.

The FLOOR OF THE NASAL CAVITY is LINED WITH THE OLFACTORY EPITHELIUM or MUCOSA.

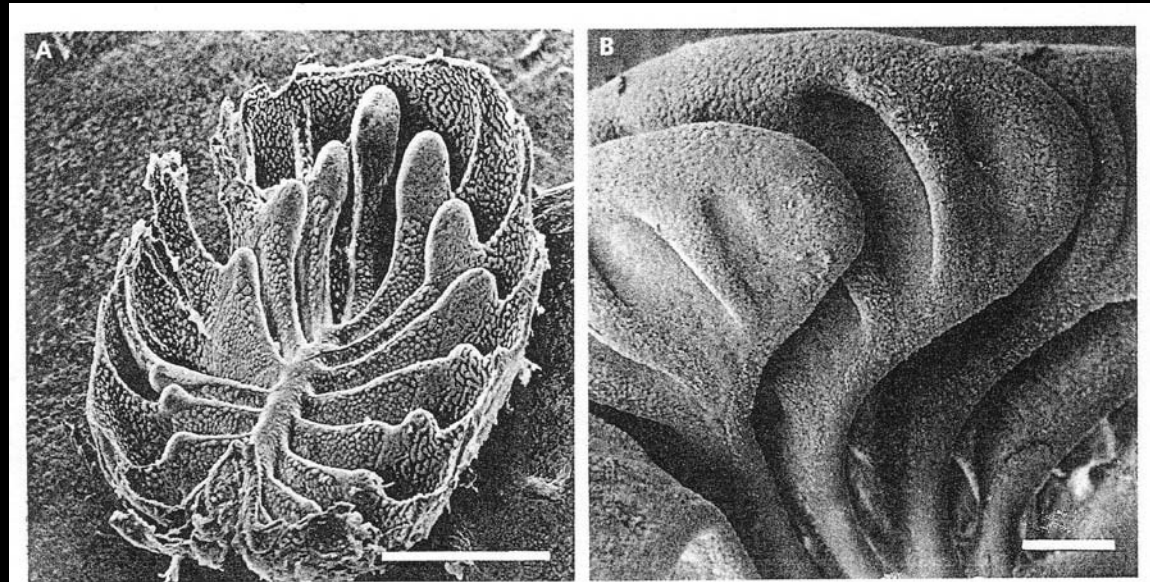
MUCOSA IS RAISED FROM THE FLOOR INTO A SERIES OF FOLDS or lamellae to form a ROSETTE.

In the majority of species, the LAMELLAE RADIATE FROM A CENTRAL RIDGE arising from the floor of the cavity.

The NUMBER OF LAMELLAE ALSO VARIES AMONG SPECIES - few in the stickleback and over 120 in eels.

The SURFACE AREA of the lamellae can be increased by SECONDARY FOLDING (salmon, sharks and lungfishes).

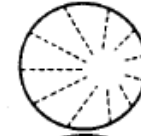
Figure 4.3: (A) Scanning electron micrograph of an olfactory rosette of the goldfish, *Carassius auratus*, showing the arrangement of olfactory lamellae and the distribution of the sensory epithelium, Scale bar = 1mm. (B) Scanning electron micrograph of olfactory lamellae of the rainbow trout, *Oncorhynchus mykiss*, showing the development of the secondary folding and distribution of the sensory epithelium. Scale bar = 300 $\mu$ m.



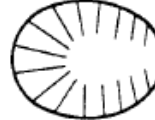
*Gasterosteus aculeatus* (2 lamellae)



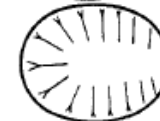
*Esox lucius* (9-18 reduced lamellae)



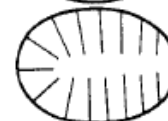
*Oncorhynchus mykiss* (13-18)



*Perca fluviatilis* (13-18)



*Phoxinus phoxinus* (11-19)



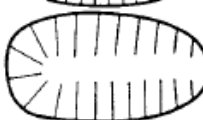
*Gobio gobio* (9-13)



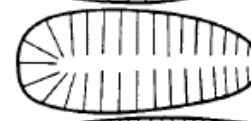
*Tinca tinca* (15-29)



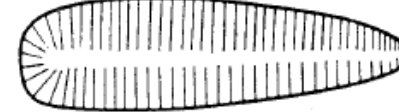
*Barbatula barbatulus* (16-24)



*Lota lota* (30-32)

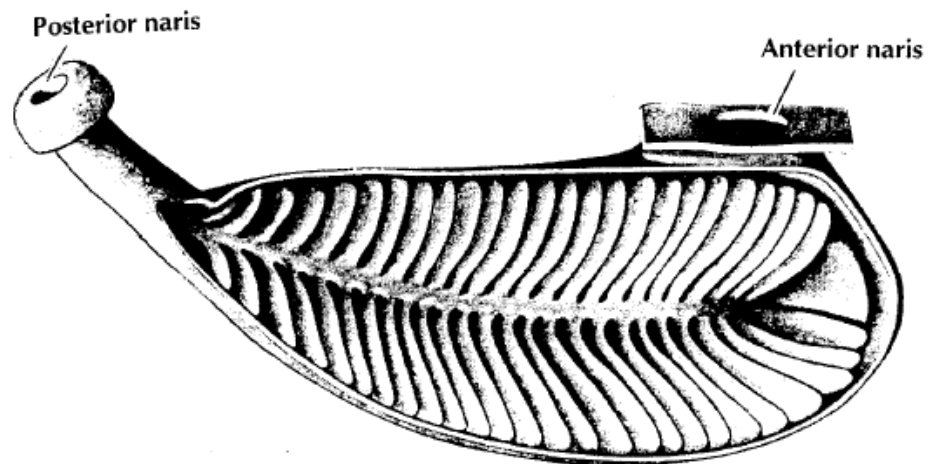
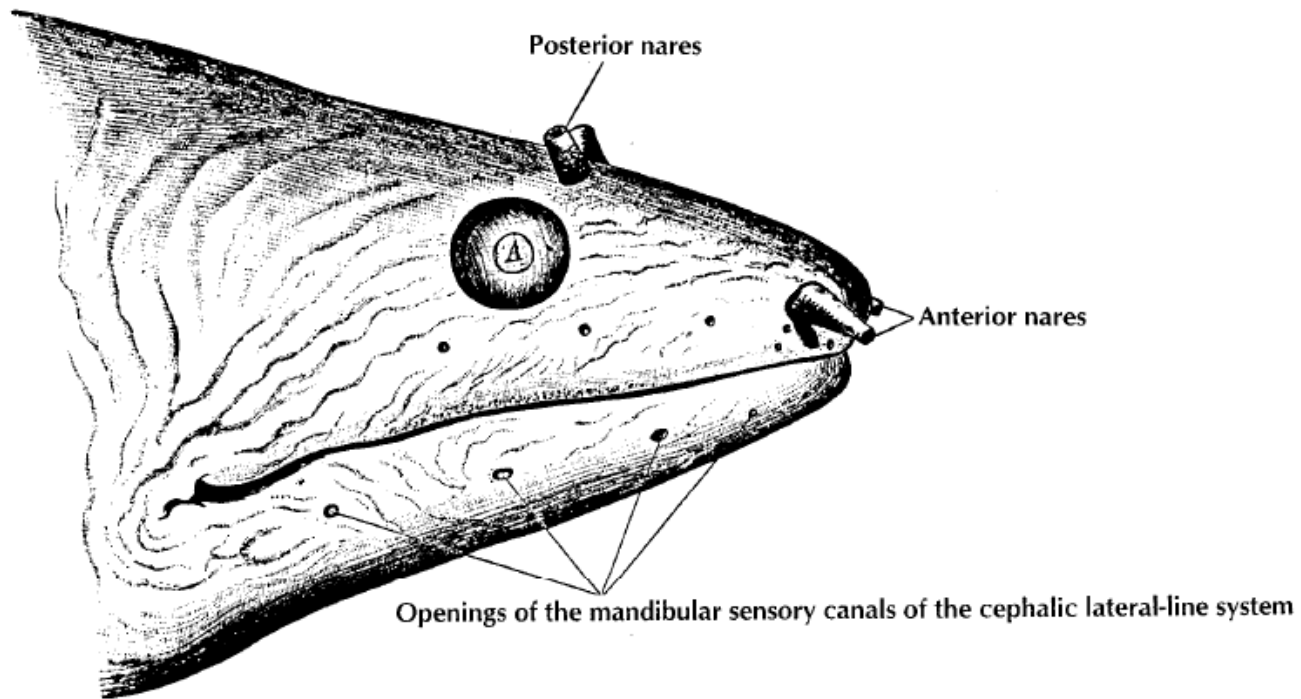


*Anguilla anguilla* (68-93)

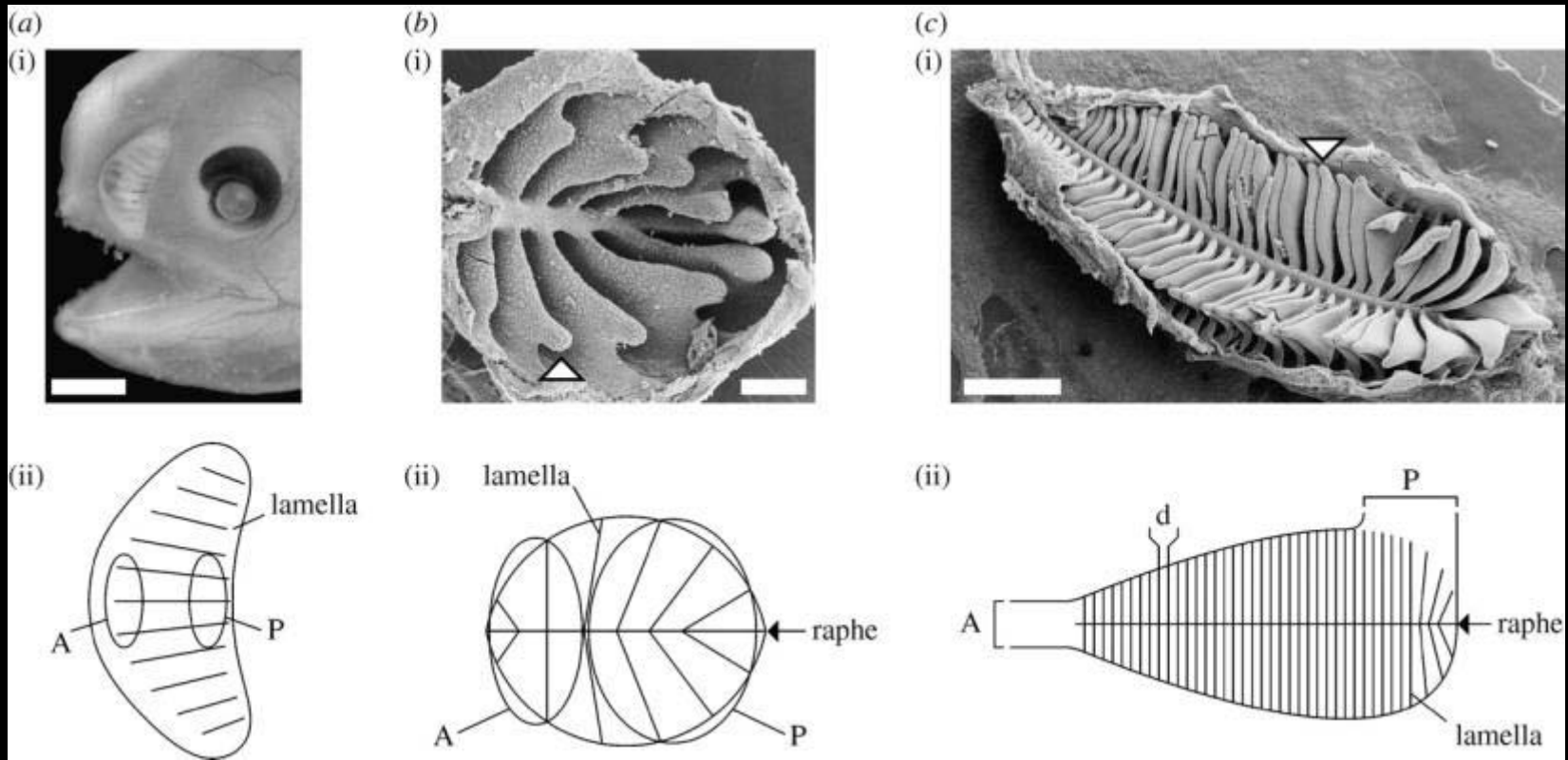


The arrangement of olfactory lamellae in ten selected species of fishes. The observed number of olfactory lamellae for each species is indicated in parentheses.





The arrangement of tubular anterior and posterior nares of an eel. Water flows into the anterior naris, across, around, and between the numerous olfactory lamellae, and back out through the posterior nares.



Three different types of olfactory lamellar array. (a) Longitudinal array of olfactory lamellae. (i) Photograph of lateral aspect of head of a preserved specimen of a male anglerfish (*Linophryne* species, total length 22mm). Scale bar, 1 mm. Photograph copyright © Natural History Museum, London (specimen catalogue number BMNH 2004.11.6.44). (ii) Plan view of olfactory chamber. (b) Rosette. (i) Electron micrograph of olfactory chamber of goldfish (*Carassius auratus*). Scale bar, 0.3mm. (ii) Plan view. (c) Elongated rosette. (i) Electron micrograph of the olfactory chamber of a European eel (*Anguilla anguilla*). Note that the raphe is gently curved rather than straight. Scale bar, 1 mm.

# Olfactory epithelium structure

These olfactory lamella are composed of TWO LAYERS OF EPITHELIUM

The epithelium is composed of COLUMNAR CELLS, which are divided into two regions, the SENSORY and NON-SENSORY REGIONS.

Cells of the sensory epithelium has various distribution patterns depending on species:

- 1) CONTINUOUS, except for the lamella margin (*Anguilla*),
- 2) SEPARATED AT REGULAR INTERVALS by non-sensory cells (*Salmoniformes*),
- 3) SEPARATED AT IRREGULAR INTERVALS with non-sensory cells (*Gyprinus*).

There are 3 main types of sensory cells:

- 1) RECEPTOR, or olfactory neuron cells,
- 2) SUPPORTING cells, and
- 3) BASAL cells.



Dissected olfactory rosette from a scalloped hammerhead shark (bottom) with a closeup of the rosette (top left) and an individual lamella (top right).



# 1. Receptor cells

ELASMOBRANCHS and the AUSTRALIAN LUNG FISH possess only MICROVILLAR receptor cells

AFRICAN LUNGFISH and LAMPREYS have only CILIATED receptor cells.

TELEOSTS have two types of receptor cells: CILIATED and MICROVILLAR.

The AVERAGE TELEOST has between 5 and 10 million receptor cells in the sensory epithelium of EACH NOSTRIL.

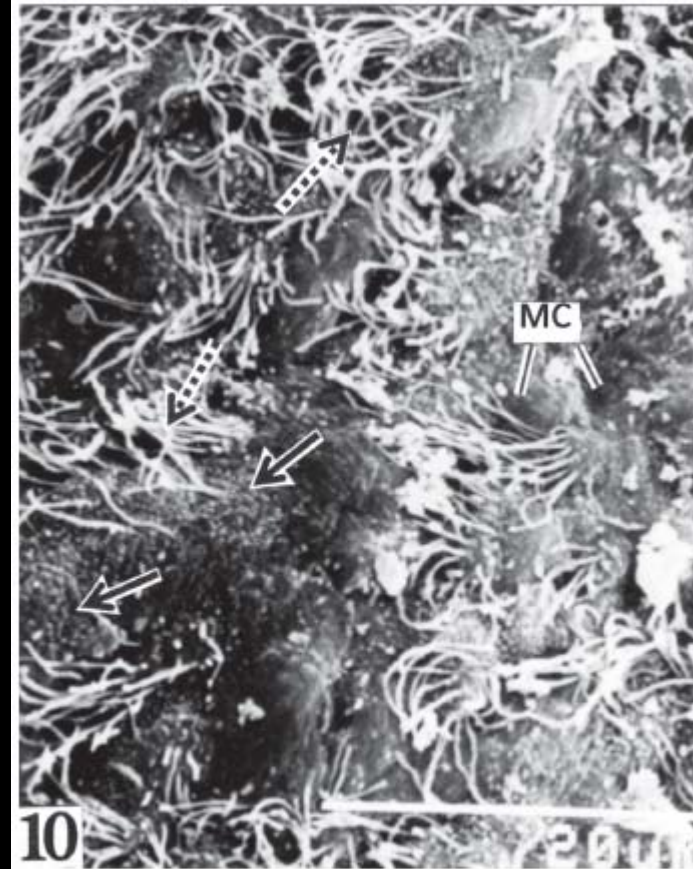
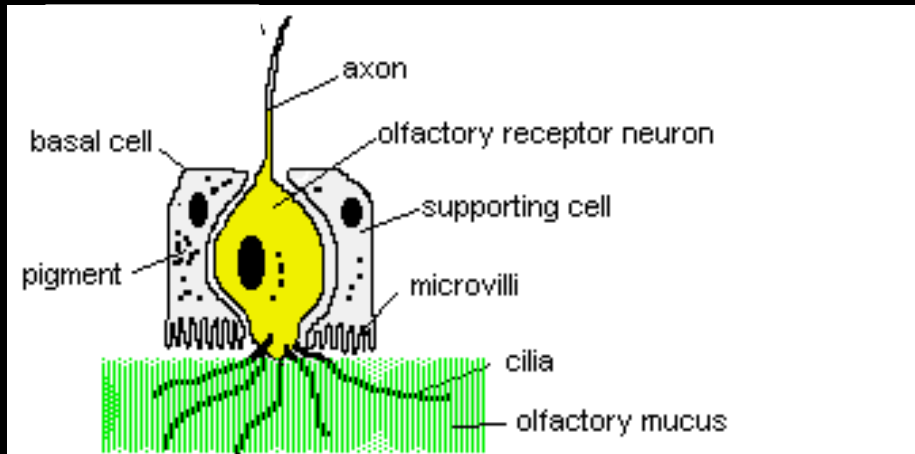
Both receptor cells have similar features.

The cell is a BIPOLAR NEURON (has two processes, an axon and a dendrite, extending in different directions from its cell body).

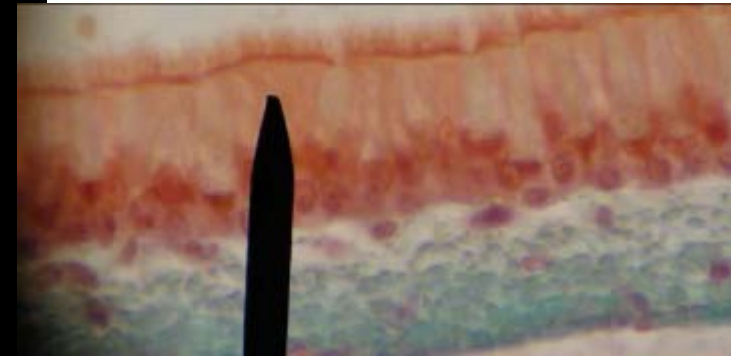
The DISTAL END of the cell forms a swelling (or olfactory knob) and PROTRUDES SLIGHTLY ABOVE THE EPITHELIAL SURFACE.

At the PROXIMAL END, the cell tapers to FORM THE AXON.

The receptor cells are RENEWED CONTINUALLY IN ADULT FISHES.



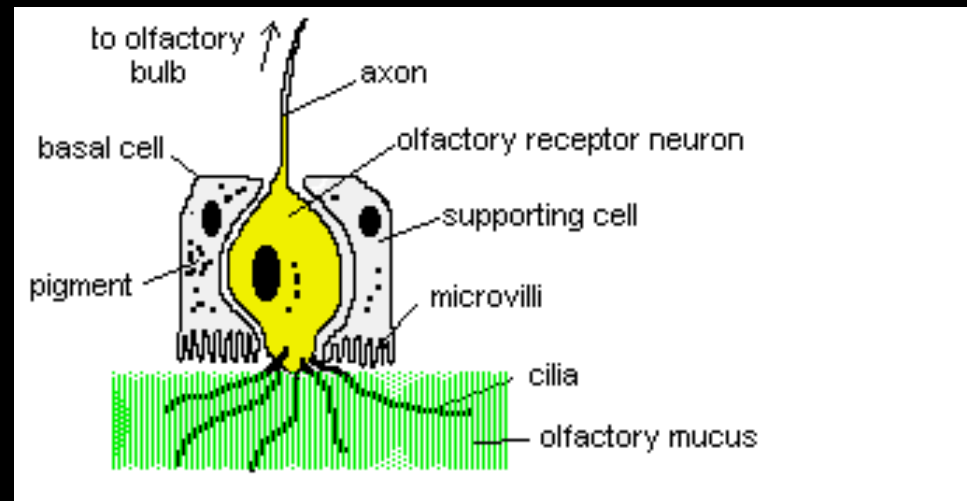
**Figure 10.** Receptor olfactory epithelium with flagellar (broken arrows) and microvillar (solid arrows) receptor cells. Note the presence of mucous cells (MC) in between receptor cells. Photomicrograph of scanning electron microscopy (SEM) and sections of olfactory epithelium of *C. catla* showing surface of cellular structure. SEM  $\times 4000$ .



# Supporting cells

The FUNCTION of the supporting cells, BEYOND SUPPLYING THE OTHER CELLS WITH MECHANICAL SUPPORT, is still UNCLEAR.

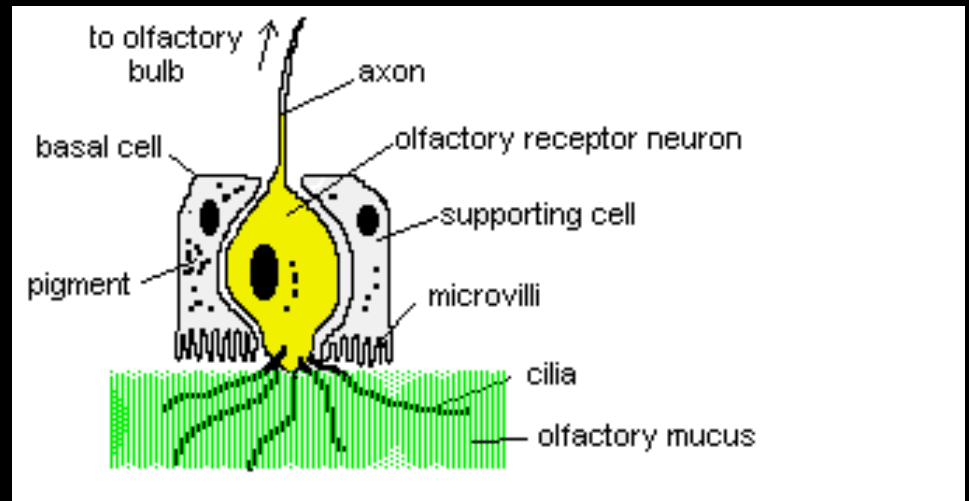
The CILIATED NON-SENSORY CELLS CREATE WEAK CURRENTS OVER THE OLFACTORY LAMELLAE. It is PRESUMED that this ASSISTS IN THE TRANSPORT OF MOLECULAR STIMULI over the olfactory organs.

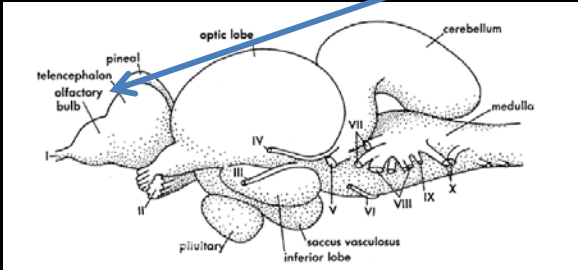
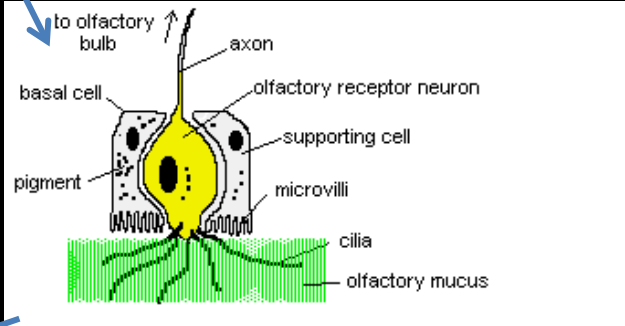
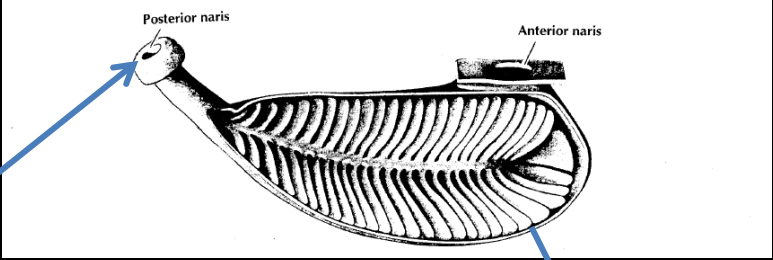


# Basal cells

The basal cells are SMALL and UNDIFFERENTIATED and found ADJACENT TO THE BASAL MEMBRANE.

It is THOUGHT THAT these cells are the PRECURSORS OF THE RECEPTOR OR SUPPORTING CELLS.





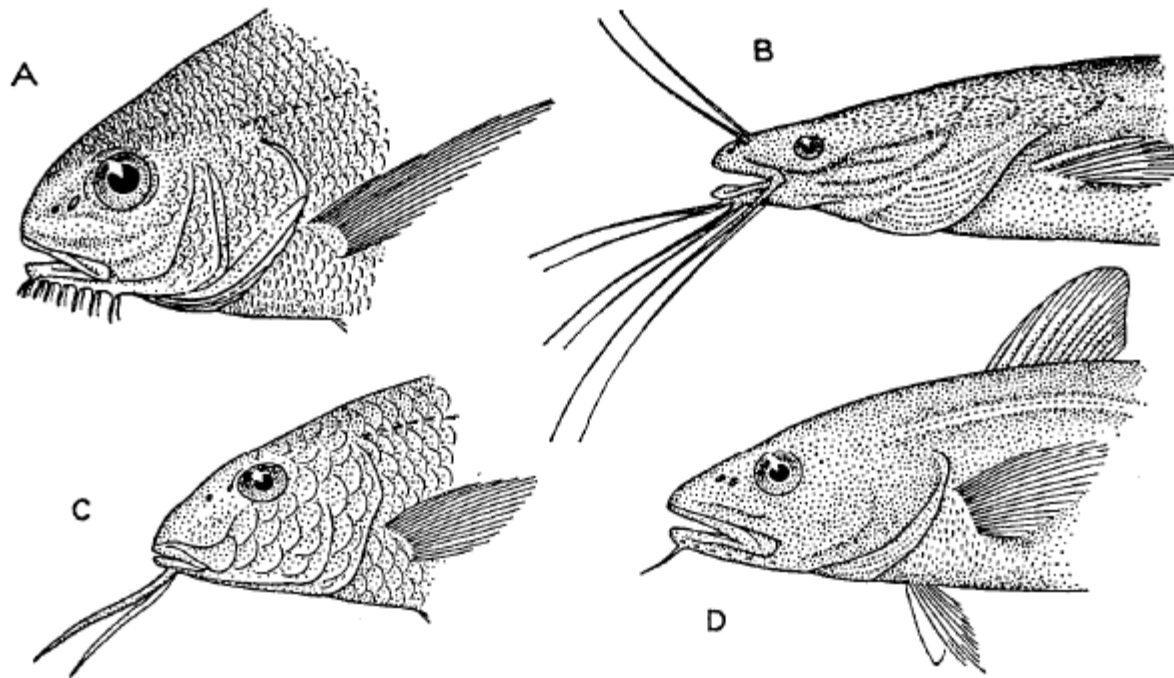
Lateral view of the brain and roots of the cranial nerves of a salmon: olfactory nerve (I), optic nerve (II), oculomotor nerve (III), trochlear nerve (IV), trigeminal nerve (V), abducens nerve (VI), facial nerve (VII), auditory nerve (VIII), glossopharyngeal nerve (IX), and vagus nerve (X)

# Gustatory system

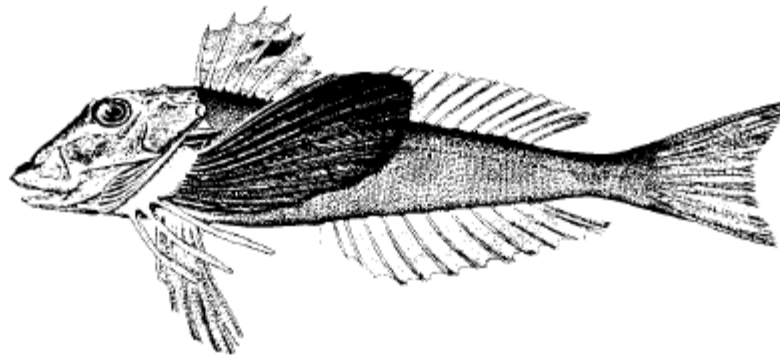
Gustation, the sense of taste, is important for the location and identification of food. Depending on the ecology of the species it can be a very highly developed sense. Eg. some minnows (Cyprinids) have a sensitivity to sugars and salts that are 512 and 184 times higher than humans, respectively.

Unlike olfactory receptors, taste receptors can be found in more than one location on the body. Besides being found in the mouth, pharynx, gill arches and skin, some fish, such as the Siluriformes have well developed barbels that have dense concentrations of taste receptor cells. Some fish, (eg. Hake Family: Gadidae) have taste buds on specialised pectoral fin rays.





Barbels of various fishes: (A) a sciaenid or drum (genus *Pogonias*); (B) a catfish (genus *Clarias*); (C) a mullet (genus *Mullus*); and (D) a cod (genus *Gadus*).

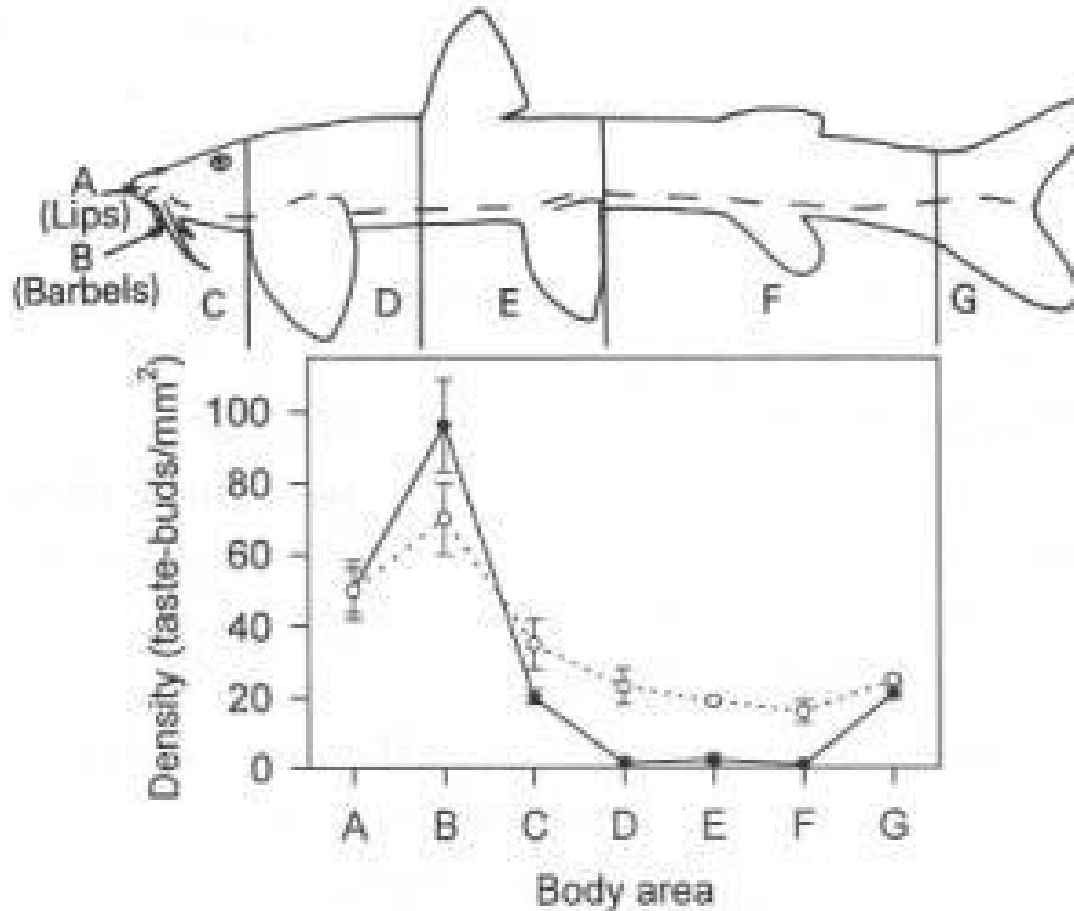


A searobin (genus *Prionotus*), with specialized pectoral-fin rays used as “feelers” to search for food on the bottom, but also, lined with taste buds, the rays are used to taste potential prey.

# Gustatory system

Taste buds can be found all over the body!

Figure 4.2: The density of taste buds found on different areas of the body of *Amphilius natalensis* viewed (●) dorsally and (○) ventrally. The dashed line separates the dorsal and ventral perspectives.



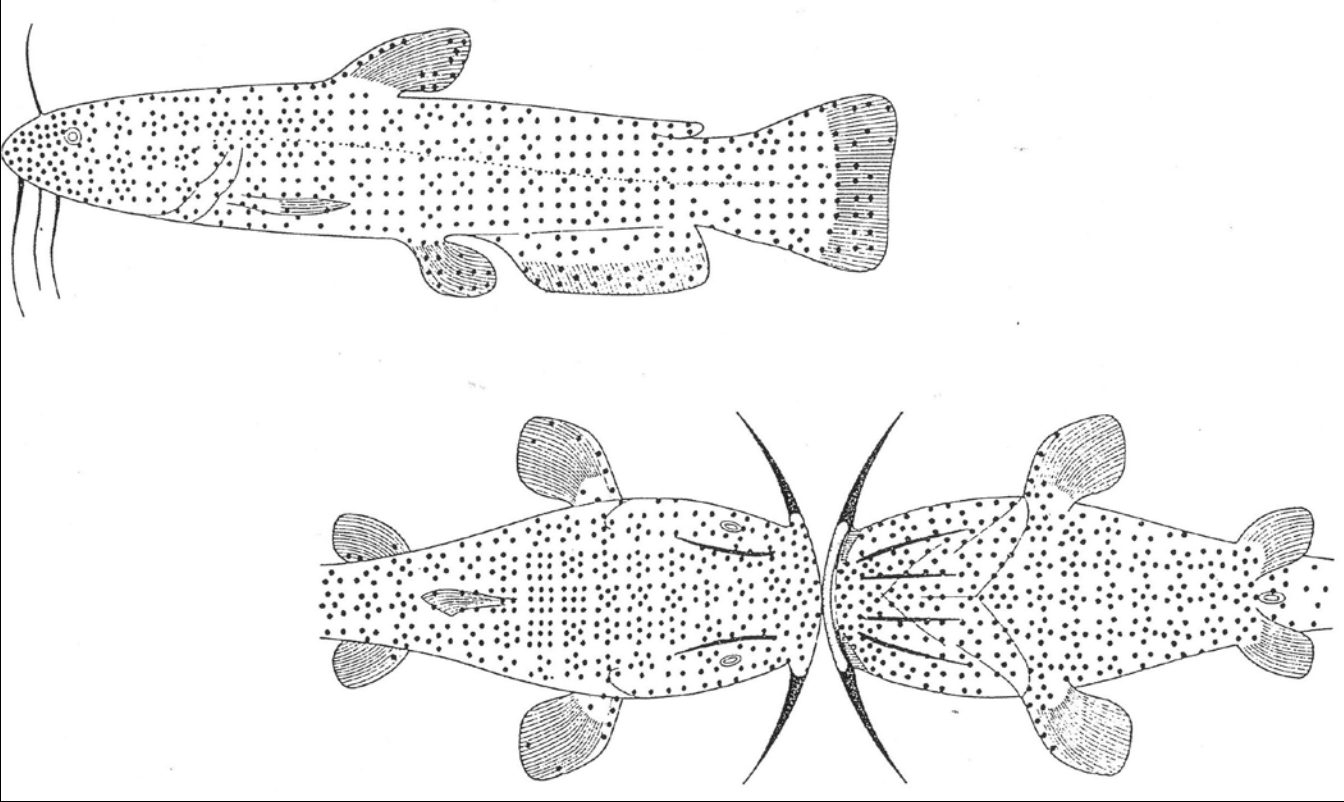
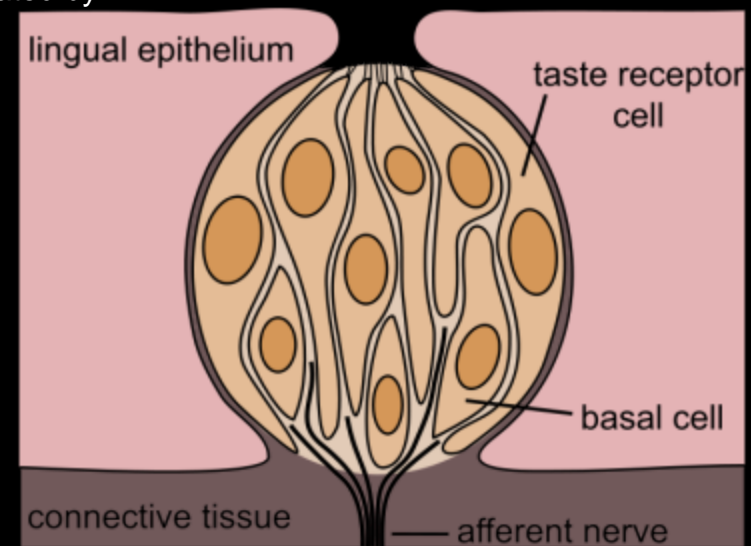


Figure 4.1: A catfish has taste buds distributed all over its body. Each dot represents 100 taste buds. Higher concentrations are found on the lips and barbells and are indicated by small dots and solid black.



In ELASMOBRANCHS the tastebuds are restricted to the MOUTH and PHARYNX.



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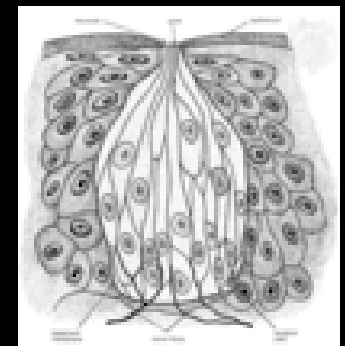
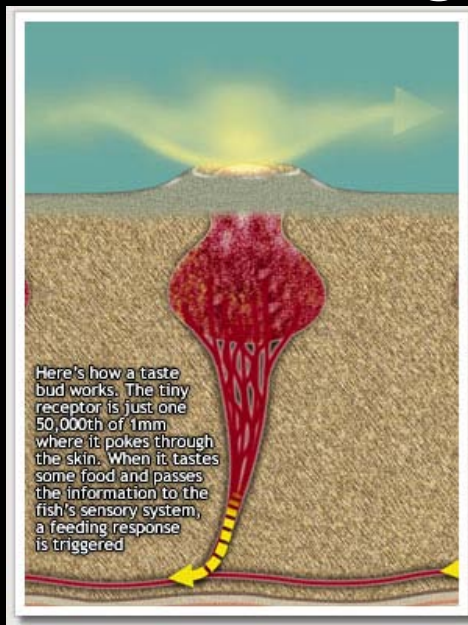
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# STRUCTURE OF A TASTE BUD

The taste buds normally have a **BULBOUS SHAPE**

**EXTEND PERPENDICULARLY** through the entire thickness of the epidermis

The **APEX OF THE TASTE BUD**, the taste bud pore, usually **PROTRUDES FROM THE SURFACE** of the surrounding epidermis



The taste bud is bulbiform in shape and varies in size from 24-75 $\mu\text{m}$  in height and 35-50 $\mu\text{m}$  in width and is made up of GUSTATORY, SUPPORTING and BASAL CELLS.

GUSTATORY CELLS are epithelial cells in a taste bud that activate sensory fibers of the facial nerve or the glossopharyngeal nerve or the vagus nerve.

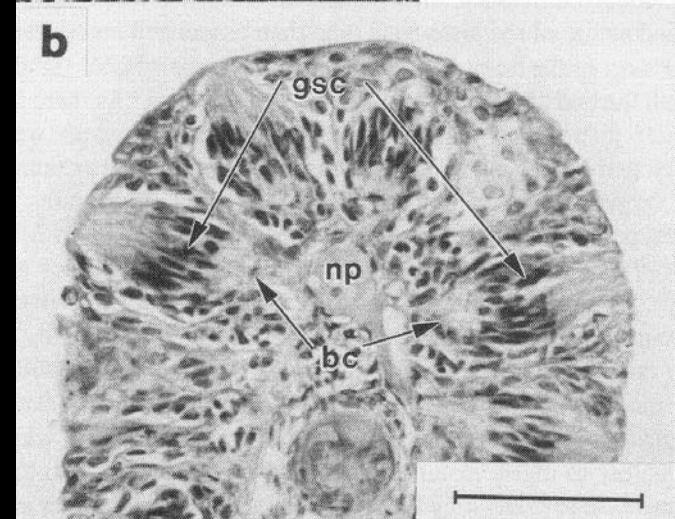
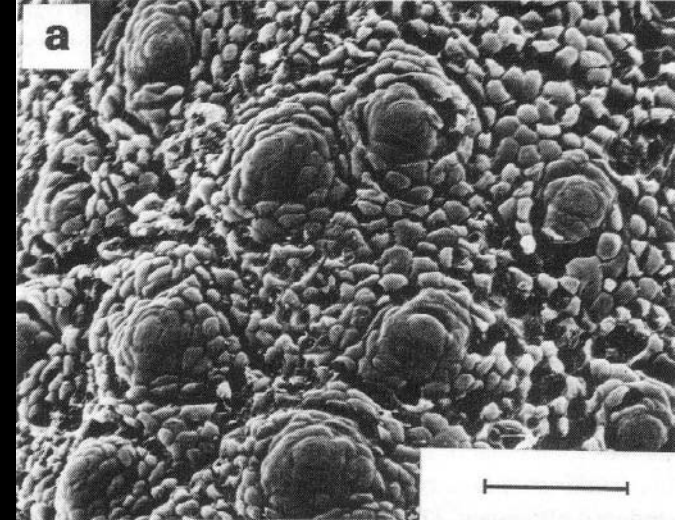
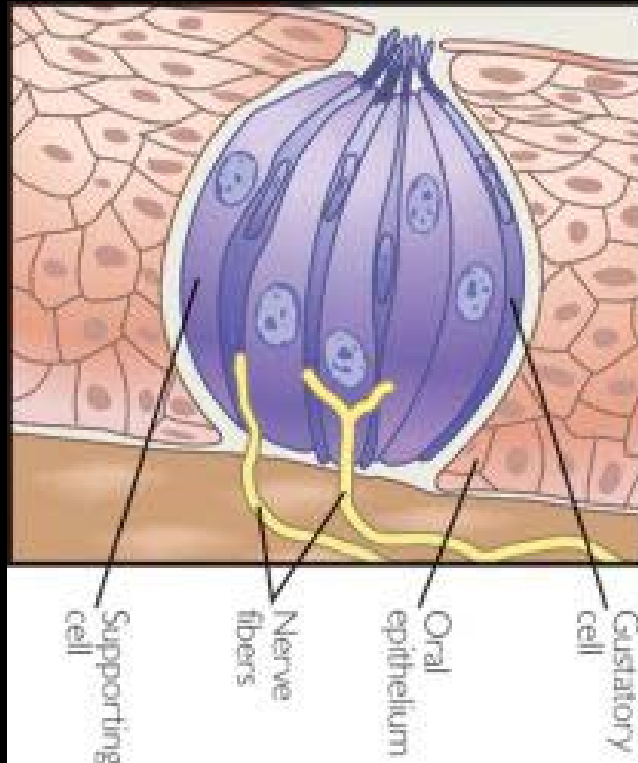


Figure 4.3: Photomicrographs illustrating the taste buds of *Amphillius natalensis*. A) A scanning electron micrograph of the dorsal lip. B) a light photomicrograph of a transverse section through a maxillary barbel. Each taste bud consists mainly of gustatory (gsc) and supporting cells. They are innervated by the nervous plexus (np) and are supported by basal cells (bc).

The GUSTATORY or receptor cells have 1 or 2 APICAL PROCESSES

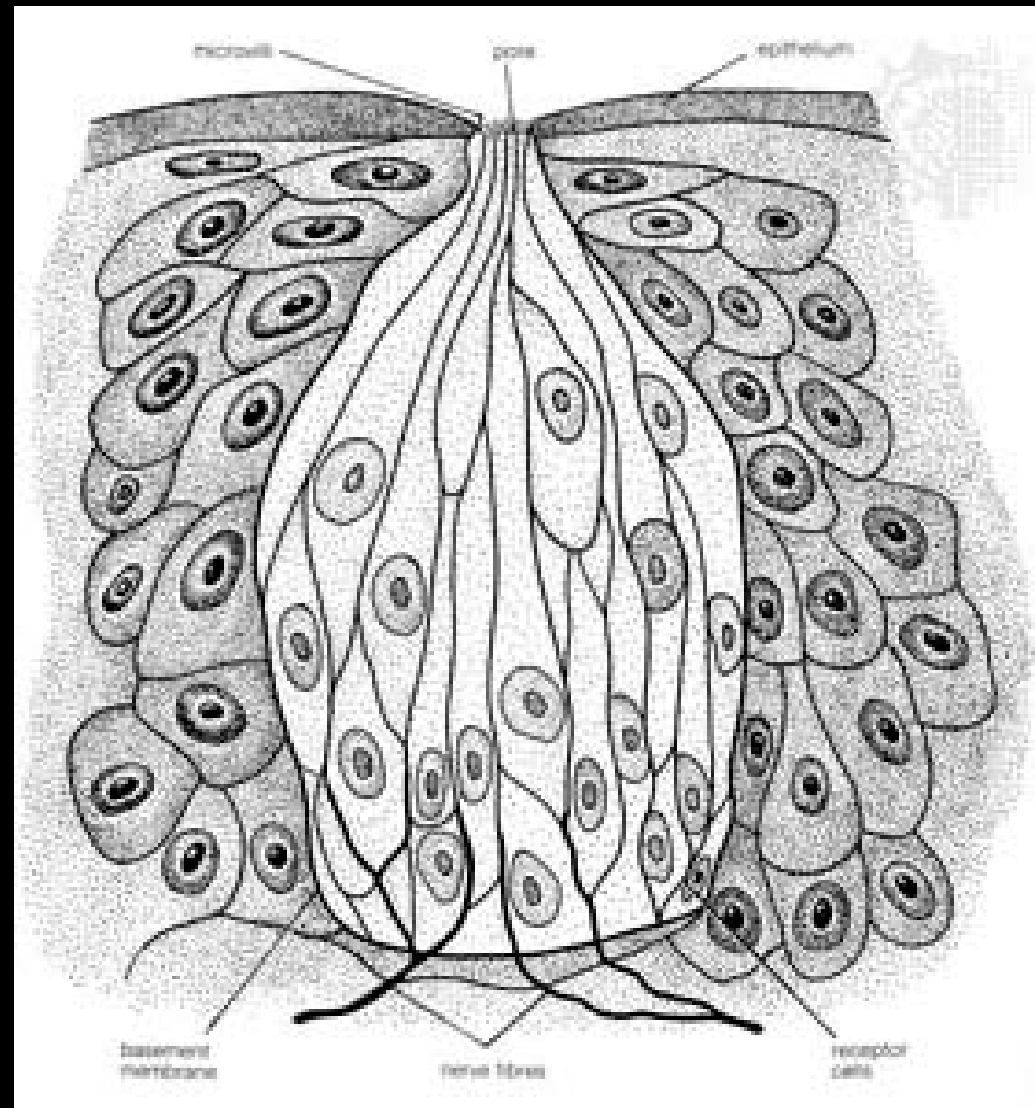
The NUMBER of gustatory cells in a taste bud VARIES CONSIDERABLY, from as few as 5 to as many as 67, depending on the species

The GUSTATORY CELL is ELONGATED, SPINDLE-SHAPED and the CYTOPLASM IS ELECTRON-DENSE

The SUPPORTING CELL is SLENDER and FUSIFORM in shape

The DISTAL REGION OF THE CELL is characterised by the presence of SECRETORY VESICLES WHICH OPEN ONTO THE SURFACE, and SECRETE A MUCOUS CAP that covers the taste bud pore

Taste buds have a LIFE-SPAN stretching between 12 and 42 days, depending on the temperature



# Cell contacts and nerves

The gustatory cells SYNAPSE with the AFFERENT GUSTATORY NERVE FIBRES.

These are the FACIAL, GLOSSOPHARYNGEAL and VAGAL nerves.

FACIAL NERVE – information from extra-oral surface - that is, from the lips

GLOSSOPHARYNGEAL NERVE - information from the anterior part of the oral cavity

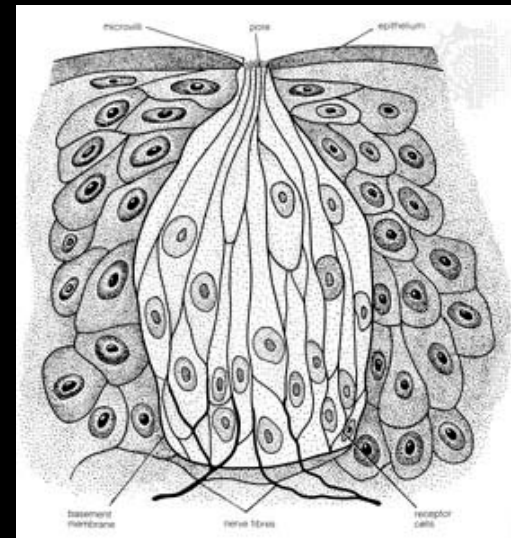
VAGAL NERVE – information from the oropharynx, or the back part of the oral cavity

In the BULLHEAD CATFISH - the taste system have TWO INTERRELATED SUBSYSTEMS

These are the FACIAL and oral or VAGAL subsystems

The FACIAL SUBSYSTEM detects chemical stimuli at a DISTANCE, and can therefore serve as a FOOD-LOCALISATION FUNCTION during the search for food

The VAGAL SYSTEM performs a DISCRIMINATORY FUNCTION, leading to the SELECTIVE INGESTION of food





# Signal transduction in olfaction and gustation

Olfactory and gustatory receptors DETECT CHEMICAL STIMULI

These STIMULI are then TRANSDUCED INTO ELECTRICAL SIGNALS, and this information is THEN TRANSMITTED TO THE CENTRAL NERVOUS SYSTEM

The BASIS OF TRANSDUCTION is LIGAND-BINDING

This is the BINDING OF AN ODOUR MOLECULE TO A SPECIFIC ODOUR RECEPTOR in the cilia or microvilli of the receptor cell

Fish are able to detect a range of CHEMOSTIMULATORY SUBSTANCES, and these include AMINO ACIDS, STEROID HORMONES, BILE SALTS and PROSTAGLANDINS

Early research on thresholds involved **behavioral experiments** in which individuals trained by reward or punishment were conditioned to select or avoid water that held the chosen chemical and then were tested on more and more diluted concentrations.

### Olfactory Thresholds of Fishes for Various Substances

<i>Substance</i>	<i>Fish</i>	<i>Threshold</i>	<i>Source</i>
Amino acids	hagfish	$10^{-6}$ to $10^{-5}$ M	Döving and Holmberg (1974)
L-methionine	lemon shark	$10^{-8}$ to $10^{-7}$ M	Zeiske et al. (1986)
Amino acids	catfishes	$10^{-9}$ to $10^{-6}$ M	Caprio (1982)
Methionine	grayling	$1.3 \times 10^{-6}$ M	Döving and Selset (1980)
Bile acids	grayling	$6.3 \times 10^{-9}$ M	Döving and Selset (1980)
Bile acids	goldfish	$10^{-9}$ M	In Meisami, 1991
Steroids	goldfish	$10^{-13}$ to $10^{-12}$ M	In Meisami, 1991
Phenylethyl alcohol	<i>A. anguilla</i>	$2.9 \times 10^{-20}$ M	In Little, 1983
Phenylethyl alcohol	rainbow trout	$10^{-9}$ M	In Little, 1983
Sucrose	<i>Phoxinus</i>	$1.2 \times 10^{-3}$ M	In Little, 1983

You can see that there is considerable variation but, in general, the **olfactory sensitivity** of fishes is comparable to that of **mammals**. For example, the **rainbow trout** (*Oncorhynchus mykiss*) has been shown to detect **phenyl-ethyl alcohol** at concentrations of  $1 \times 10^{-9}$  molar, which is on the same order of sensitivity as humans.

# Chemoreception and fish behaviour

Chemoreception is IMPORTANT IN THE BEHAVIOURAL INTERACTIONS OF FISH.

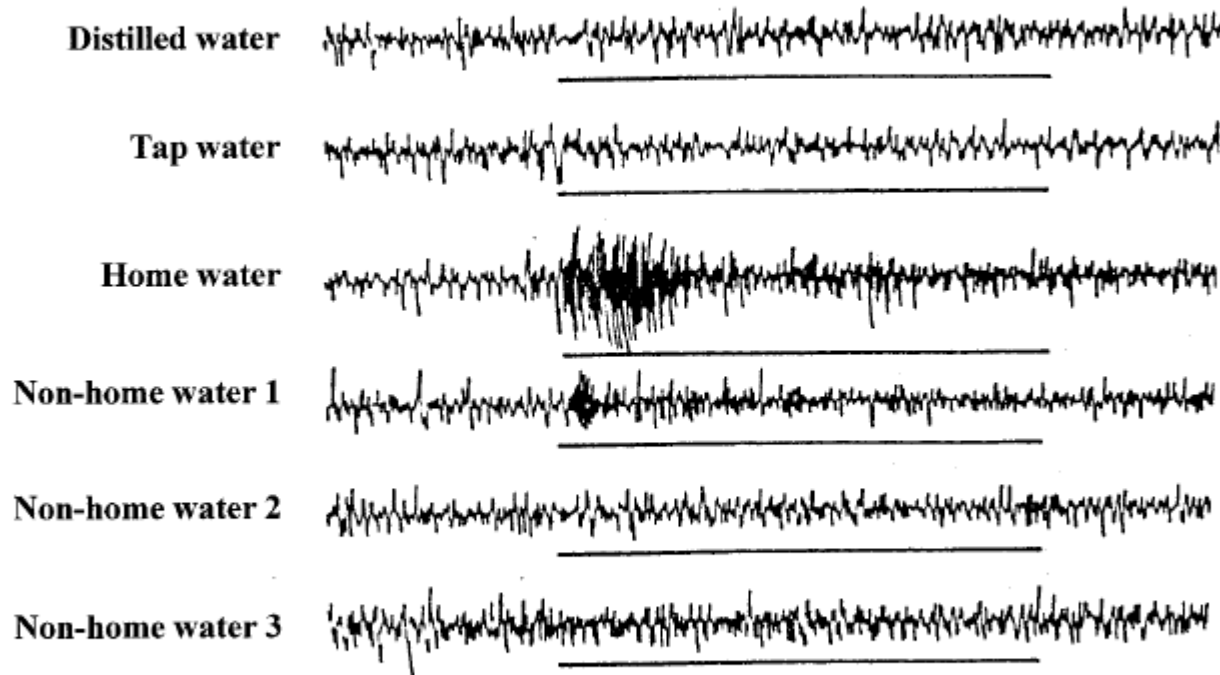
The most important are:

- HOMING OF SALMON – philopatry and imprinting
- HORMONES, PHEROMONES AND REPRODUCTION – eg elicit courtship behaviour in fish
- INTRA- AND INTERSPECIFIC INTERACTIONS - Schreckstoff
- FEEDING – eg feeding stimulants



# Homing of salmon

**Migration:** Olfaction has been shown to play key roles in the migration of salmonids and freshwater eels (*Anguillidae*). In the former case, the specific odorants are imprinted on the young during development and early rearing.

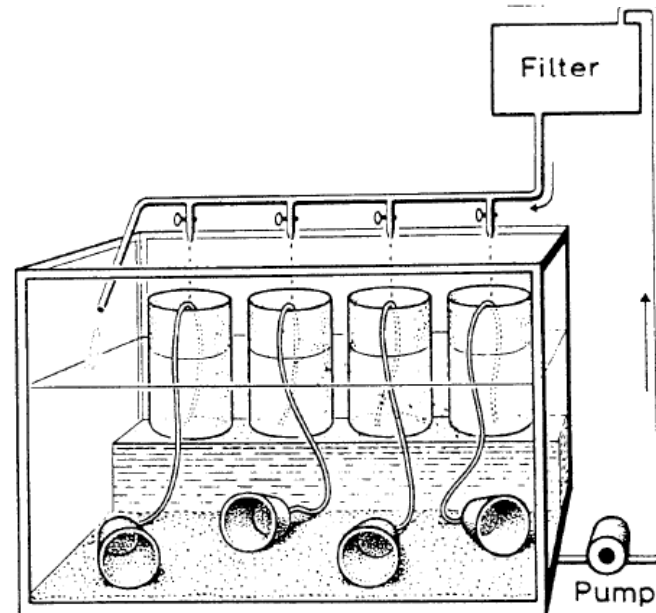


Effects of infusion of different waters into the olfactory chamber measured by electroencephalogram activity in the olfactory bulb of an adult spawning salmon.



# Cichlid reproduction

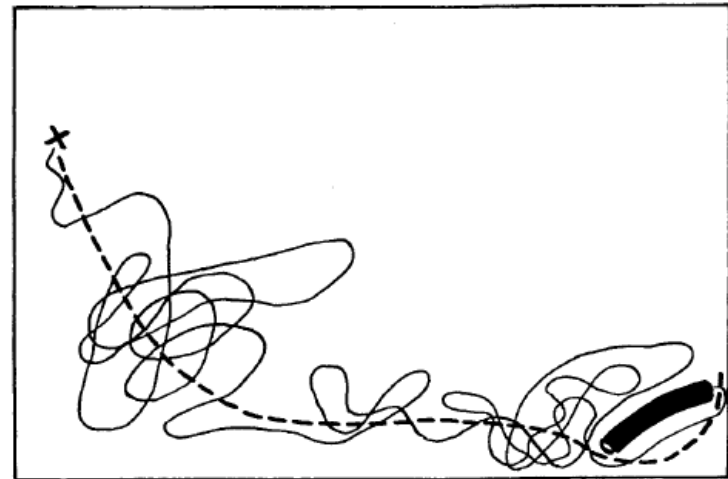
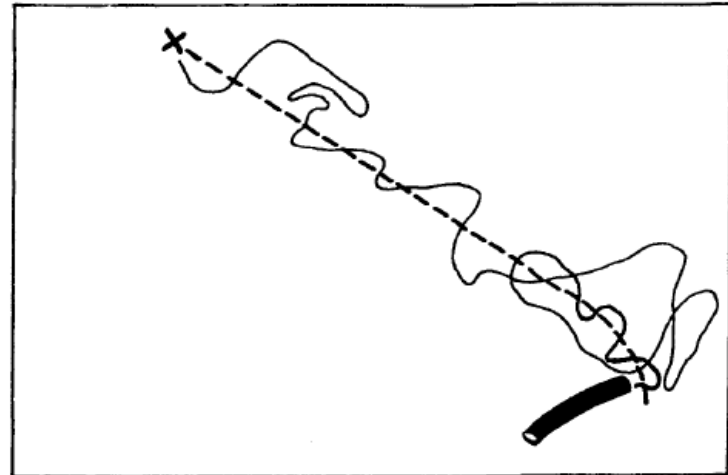
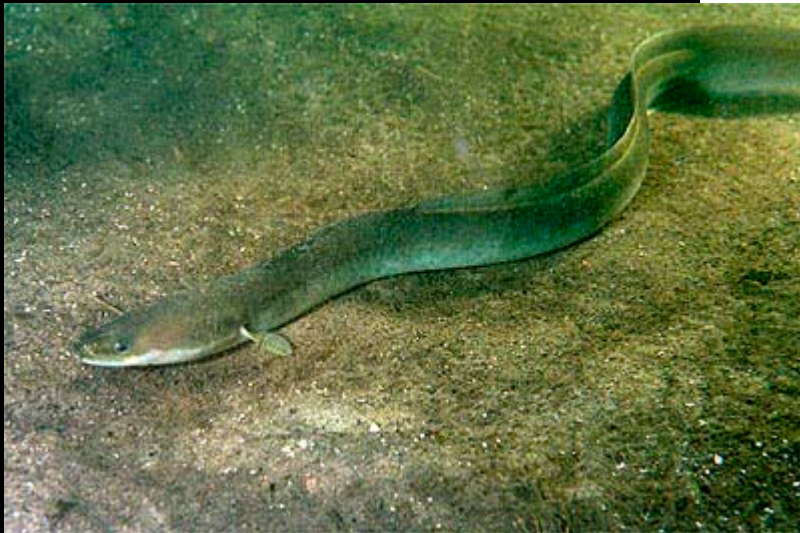
One of the clearest examples of the role of **chemoreception** in **parental behavior** comes from work on the **cichlid** *Hemichromis bimaculatus* (often called the **jewel fish**). Pairs were allowed to spawn in one of four clay flowerpots. After spawning or hatching, the pot containing the eggs and fry was removed and another put in its place. The pot with the developing embryos was placed randomly in one of four white cylinders from which water was supplied to the tanks (through the clay pots in the tank). Once the eggs were hatched, the parents always gathered around the pot that came from the cylinder containing their young. Further, they displayed parental behavior typical of the species even though no young were visually present. The response lasted the full three weeks typical of the period of their parental behavior. Finally, when the late stage young were replaced with newly hatched embryos, the female parent switched her behavior to that appropriate for newly hatched young, continually fanning the pot and imaginary embryos with her pectoral fins to keep oxygen levels high.



Experimental arrangement to test the preference of breeding cichlids (genus *Hemichromis*) for water carrying the odor of their offspring.

# Finding food

Pathways of aquarium held eel in search of an odour to which it had been conditioned



Pathways of an aquarium-held eel (*Anguilla anguilla*) following a trail of phenyl-ethyl alcohol, laid down by means of a pipette, leading to the source of the odor in the hollow tube. In the experiment at the top, localization of the source of the odor required 2 minutes; in the bottom experiment, 4 minutes were required (distance 35 cm).

- End of lecture