

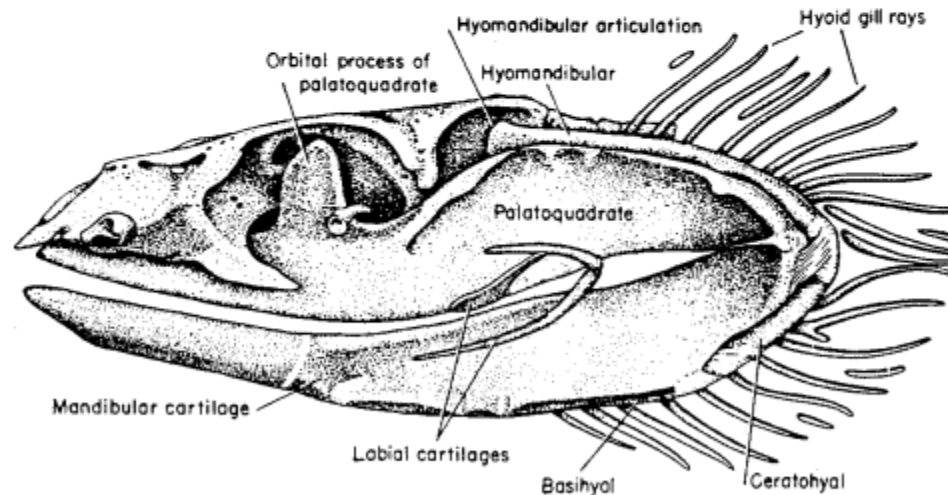
Lecture 8 – Head and Jaw osteology

3. THE JAWS OF PRIMITIVE JAWED FISHES

The earliest kinds of **jawed fishes** are all extinct, belonging to a group called the **Placodermi**. We have no living remnants of these animals to look at but we do have an incredibly diverse fossil record.

We know that the jaws of these earliest jawed fishes were made of **endochondral bone** or **replacement bone**; that is, they were constructed of bone that was first laid down as cartilage. To see the morphology of these elements in living fishes we can look at chondrichthyan fishes (i.e., sharks and their allies), which inherited endochondral jaws from the earliest jawed fishes.

CRANIAL SKELETON OF A SHARK

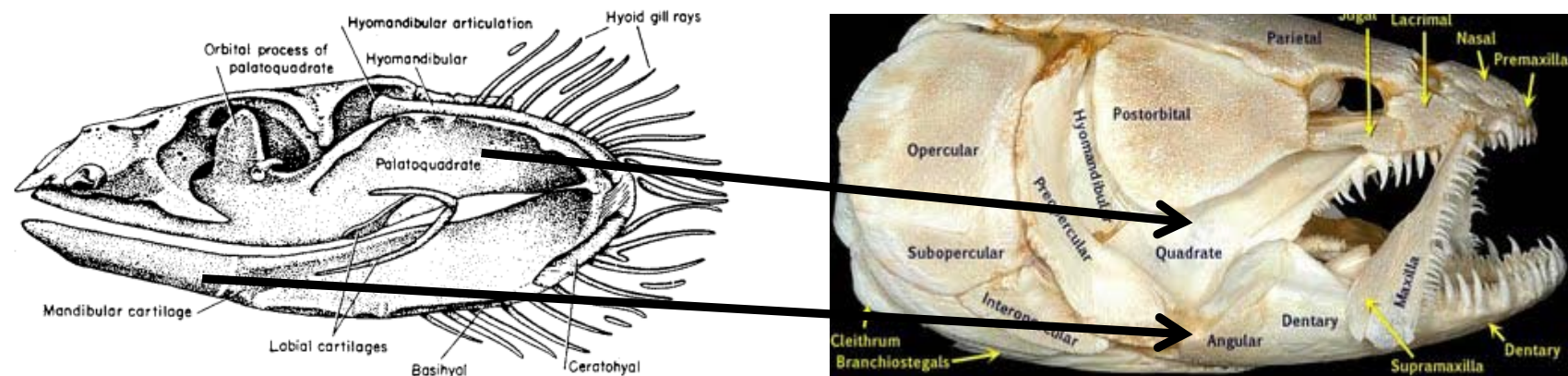


In Chondrichthyes, the upper jaw is called the **palatoquadrate cartilage**; the lower jaw is called the **mandibular cartilage** or sometimes **Meckel's cartilage**.

Now, if we continue to trace the evolution of jaws from these ancient forms to bony fishes (**Actinopterygii**) as well as to other more highly evolved vertebrates (**Sarcopterygii**), we see some significant changes. It turns out that the jaws of these more derived vertebrates are made up of entirely different elements, elements that are not pre-formed in cartilage but are instead dermal in origin.

The old endochondral elements that once formed the jaws become internalized and take on other functions that are less directly related to feeding: the **palatoquadrate cartilage** evolves to form elements that make up part of the suspensorium, that functional unit of the cranium that supports or suspends the jaws: part of it becomes the **palatine** bone and part forms the **quadrate**. But in primitive tetrapods it comes to form part of the roof of the mouth (i.e., the palate); and eventually, in mammals, part of it forms the **incus**, one of the three bony ossicles of the middle ear.

The **mandibular cartilage** also takes on suspensory functions in derived fishes; that is, it comes to form an element called the **articular** that connects to the quadrate bone of the suspensorium to suspend the lower jaw. In mammals, part of it becomes the **malleus**, another of the three bony ossicles of the middle ear.



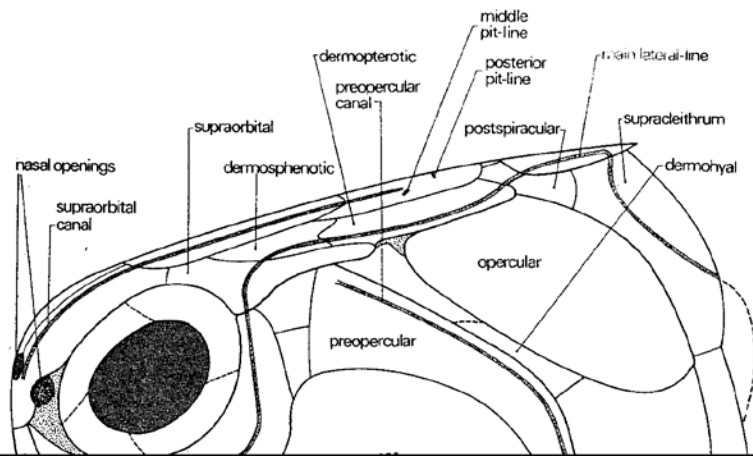
4. THE DERMAL JAWS OF ACTINOPTERYGIANS AND SARCOPTERYGIANS

So, these **endochondral** bones are lost as jaws, but they are replaced with **dermal** elements: thick, overlying bony plates, homologous to the primary dermal armor of extinct pteraspidomorphs, come to lie in a position surrounding the mouth.

The upper jaw consists of two dermal elements: **premaxilla** and **maxilla**.

The lower jaw is called the **dentary**.

SKULL OF A PRIMITIVE ACTINOPTERYGIAN FISH



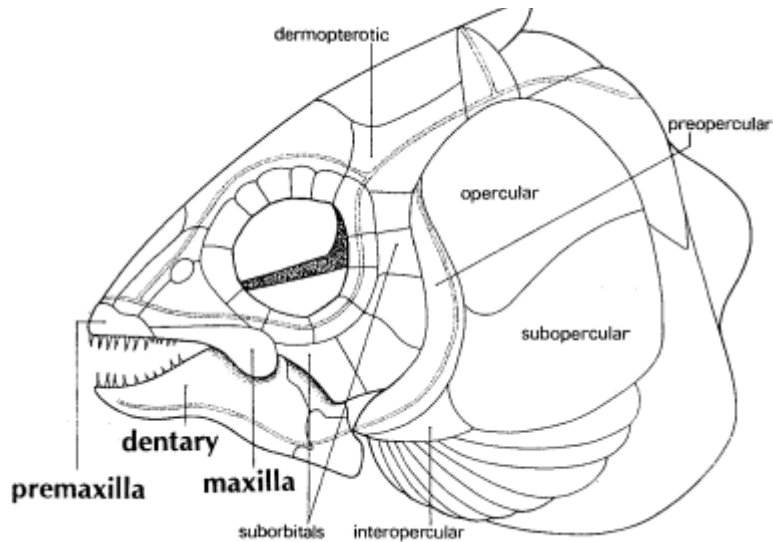
In the most primitive actinopterygians, the maxilla was a large bone, expanded posteriorly and sutured to the elements of the cheek (largely attached to the preopercle). It was **immobile** relative to the cranium.

More derived fishes

(Ray finned fishes)

In more derived actinopterygians, the posterior end of the maxilla has lost attachment to the cheek and is now **mobile** relative to the cranium. Now, when the mouth is opened, the maxillae, one on each side, rotate forward and downward to close off the corners of the mouth, providing a convenient way to help prevent the escape of prey.

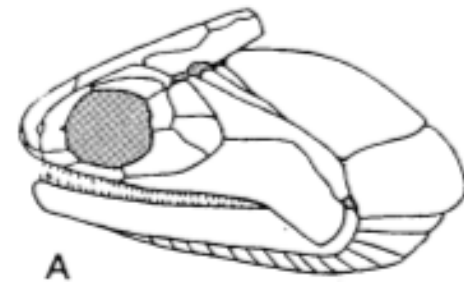
SKULL OF A DERIVED PRE-TELEOSTEAN ACTINOPTERYGIAN



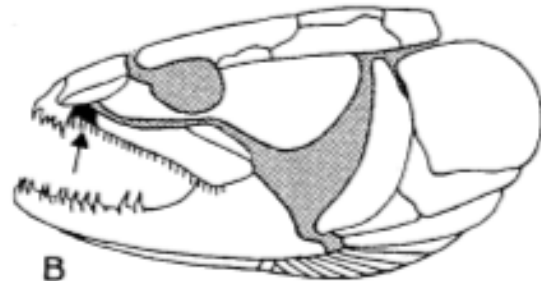
But when we turn now to **teleosts**, we find additional changes that further increase upper jaw mobility. In addition to the posterior end of the maxilla being freed from the cheek, we find for the first time, a **ball and socket joint** developed between the head of the maxilla and the palatine bone. This new **highly mobile joint** is thought to be a real improvement over the simple connective tissue hinge found here in more primitive actinopterygians.



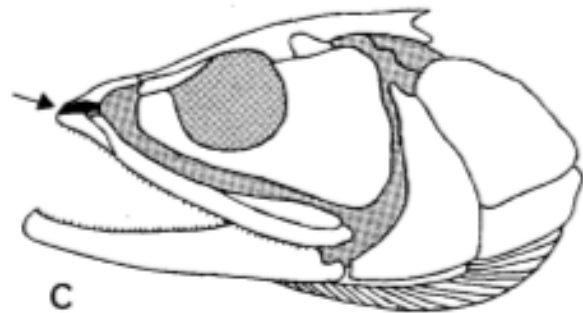
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A



B



C

SKULLS OF ACTINOPTERYGIANS:
A. Sturgeon ancestor; B. *Amia*; C. *Elops*.

6. FUNCTIONAL REPLACEMENT OF THE MAXILLA IN TELEOSTS

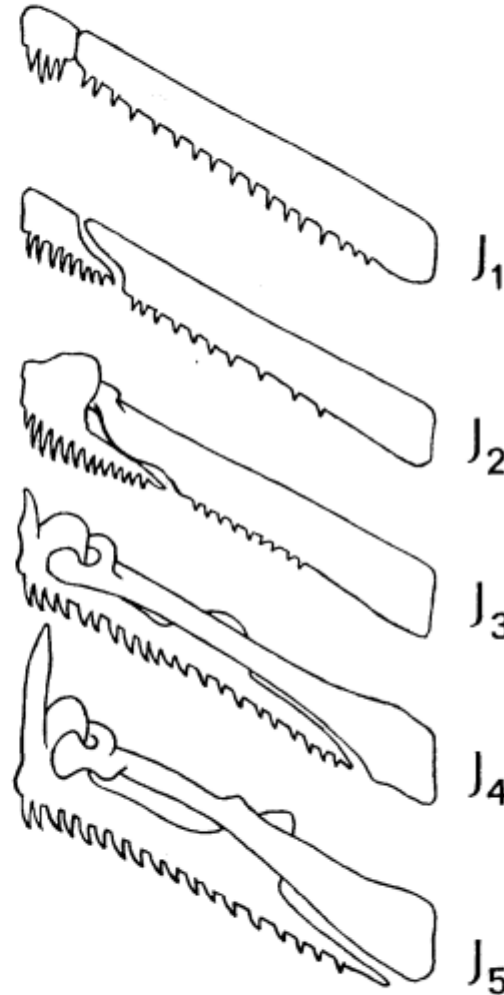
Further, additional changes appear as teleosts themselves evolve: in primitive teleosts, the **premaxilla** is small and anterior in position; both the premaxilla and maxilla bear teeth but the major tooth bearing bone is the **maxilla**.

As teleosts evolve, the premaxilla begins to elongate and overlap the maxilla; it begins progressively to take on more of the tooth-bearing function of the upper jaw.

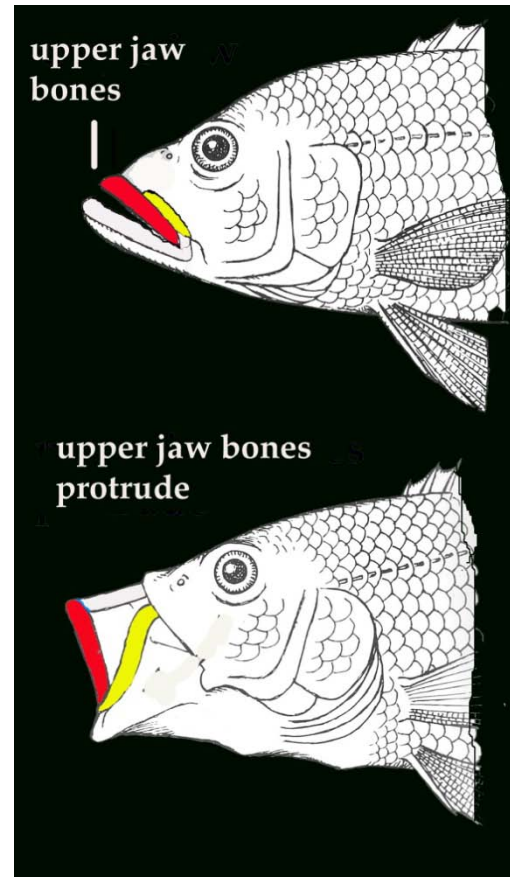
Eventually, the premaxilla fully excludes the maxilla from the gape of the mouth and becomes the only tooth-bearing element of the upper jaw.

In the most highly evolved teleosts, the anterior end of the premaxilla develops what's called an "**ascending process**" that extends upward and backward to overlap the snout region of the head. This ascending process functions as part of a highly mobile upper jaw that allows the jaw to be protruded away from the snout; the maxilla behind, which has lost its old tooth-bearing function, now functions as a level to help thrust the premaxillae forward.

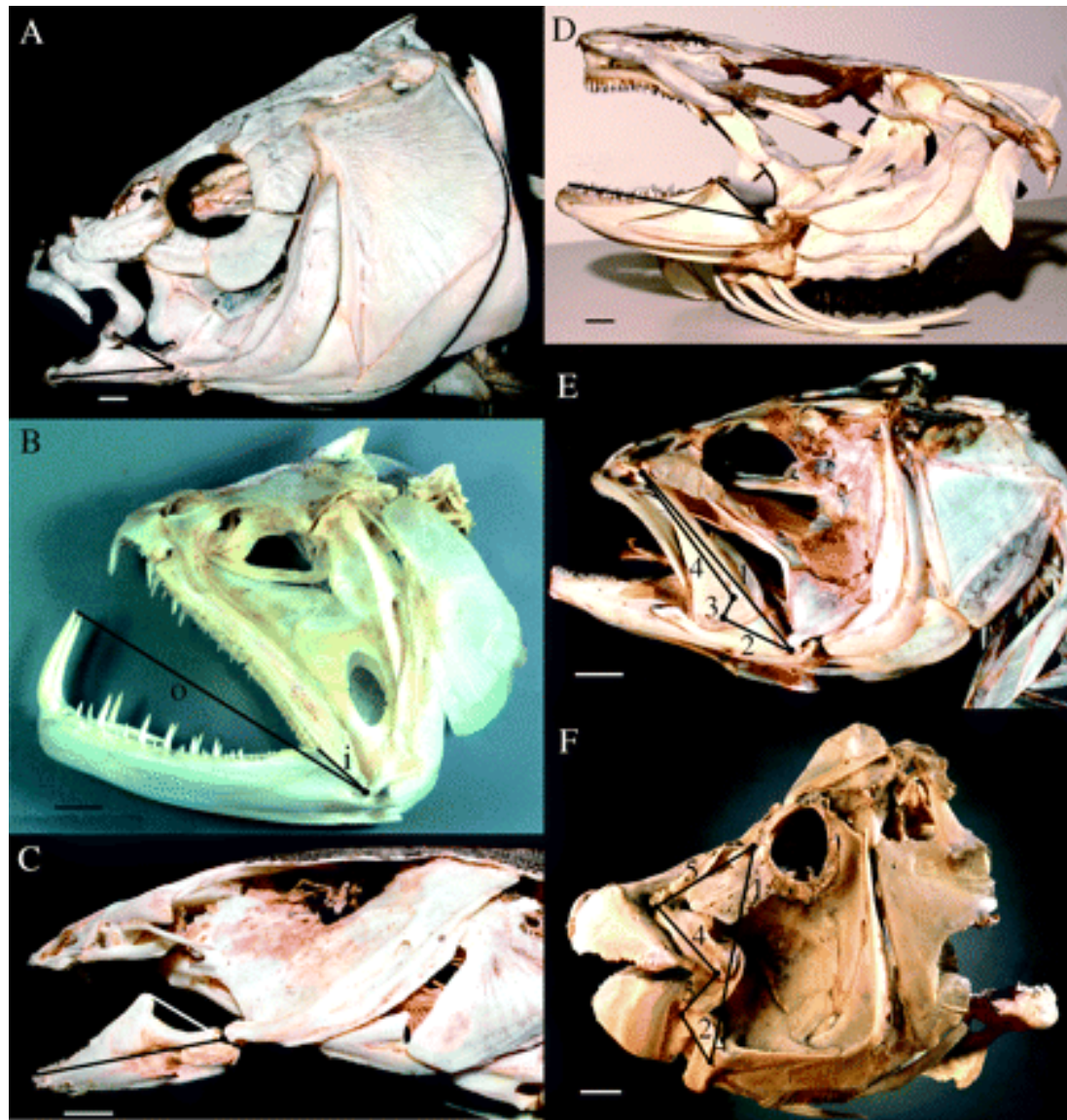
While all this is happening, the original bony connection of the premaxillae with the snout in preteleosts was replaced with a much more flexible cartilaginous and connective tissue hinge—all providing for a **highly mobile upper jaw**.



Representation of types of associations between the two upper jaw bones of teleostean fishes, diagrammatic. In the primitive condition, J₁, premaxilla to the left, maxilla to the right in series; in the most derived condition, J₅, the two bones are in tandem.



The variability of the jaw structure of bony fishes provides an explanation for the extensive **adaptive radiation** in the group and why they are so diverse and occupy almost every aquatic niche available.



Skull diversity (A) carp, *Cyprinus carpio*, (B) vampire characin, *Hydrolycus scomberoides*, (C) catfish *Arius felis*. (D) cod *Gadus morhua*. (E) large-mouth bass, *Micropterus salmoides* (F) The parrotfish *Scarus guacamaia*.

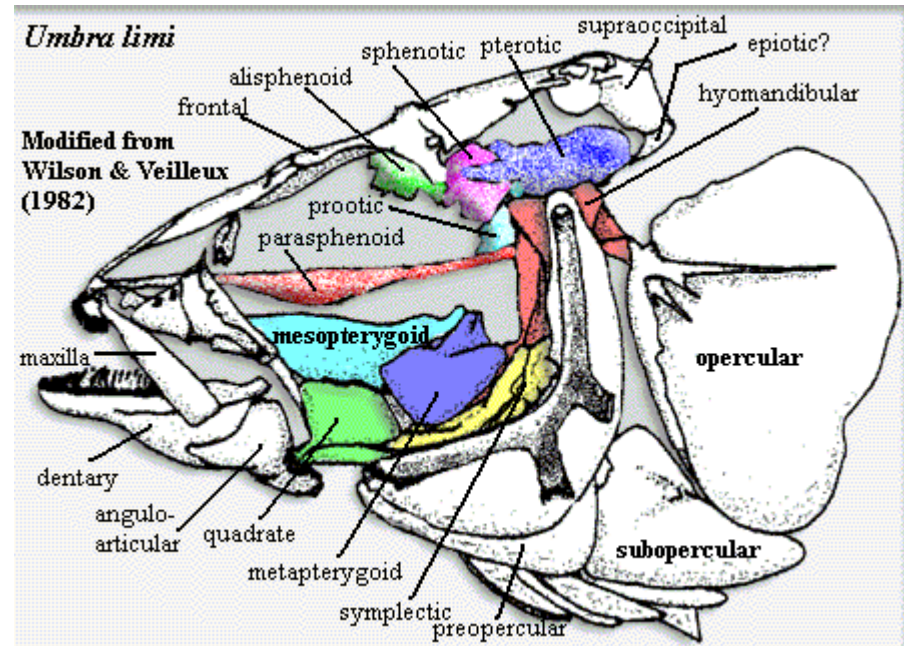
Scale bar = 10 mm

WESTNEAT 2004

From an evolutionary standpoint, fishes were the first animals to develop bony jaws. Versatile jaws and multiple feeding strategies allowed fishes to fill, or radiate into, a diverse range of niches.

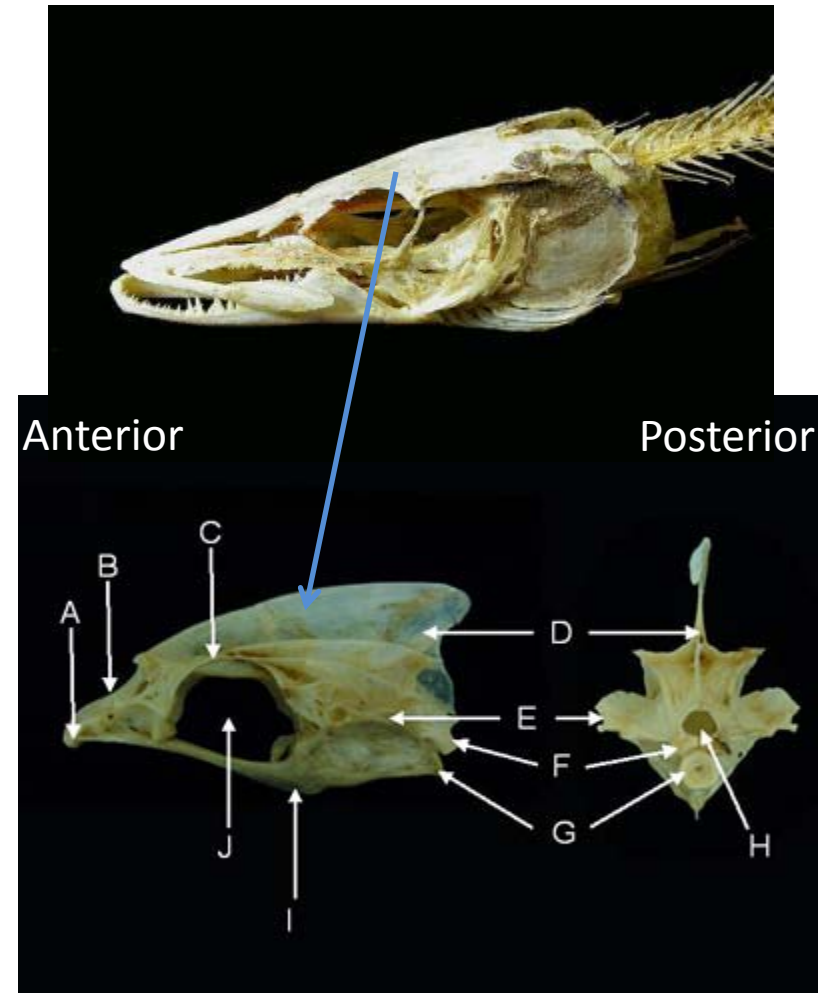
They have evolved to feed in all possible ways – sucking, biting, scraping, nipping, crushing etc.

The head of a teleost has 5 main regions: Cranium, jaws, cheeks, hydroid arch, opercula.



The head of a fish has five main regions

- 1) The **CRANIUM** is composed of the bones providing direct support and protection to the brain and the visual, olfactory, and auditory organs. Below the cranium is the parashenoid bone.
- Parasphenoid plays a role in the jaws as it acts as a hard palate

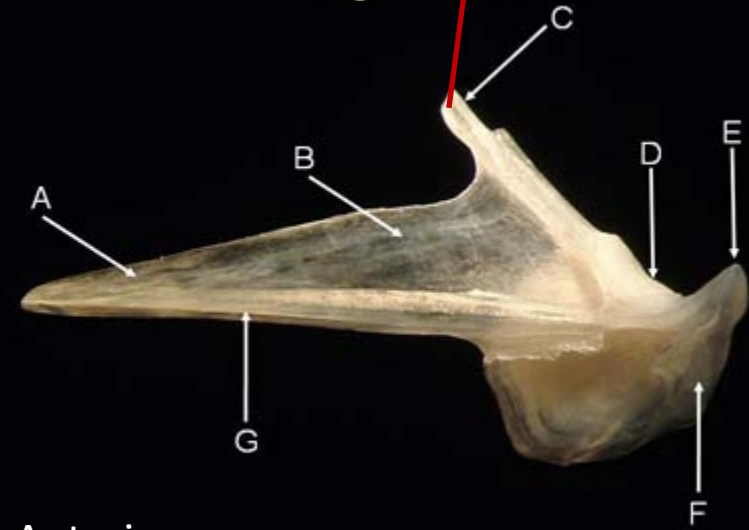
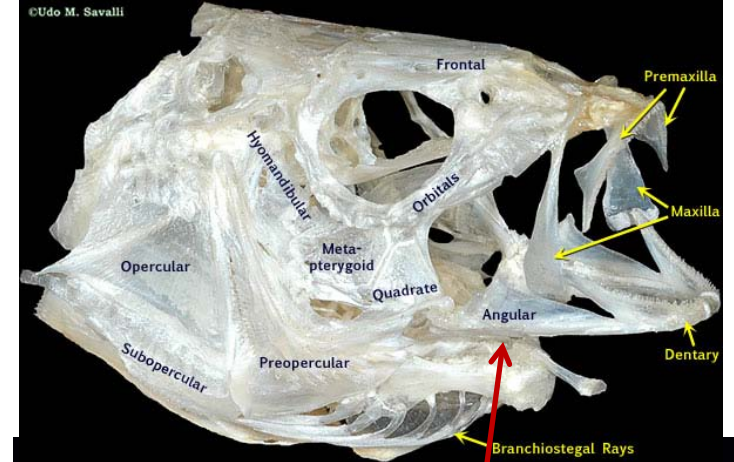


Features of the neurocranium sensu lato (from *Caranx melampygus*, lateral aspect, left, and posterior aspect, right). A = prevomer, B = ethmoid, C = frontal, D = supraoccipital, E = pterotic, F = exoccipital, G = basioccipital, H = foramen magnum, I = parasphenoid, J = orbit.

The five main regions

2) The JAWS

- **Lower Jaw** – has an Angular articular and dentary bone
- **Angular articular**- The paired bones form the posterior part of either side of the lower jaw and articulate with the suspensorium. In teleosts, the angular is typically triangular with an anterior process fitting between the coronoid and ventral processes of the dentary. The lower jaw pivots on the quadrate facet of the angular, which fits between the lateral and mesial condyles of the quadrate. Moray eels (Muraenidae), surgeonfishes (Acanthuridae), and pufferfishes (Tetraodontidae) have distinctive angulars.



Anterior

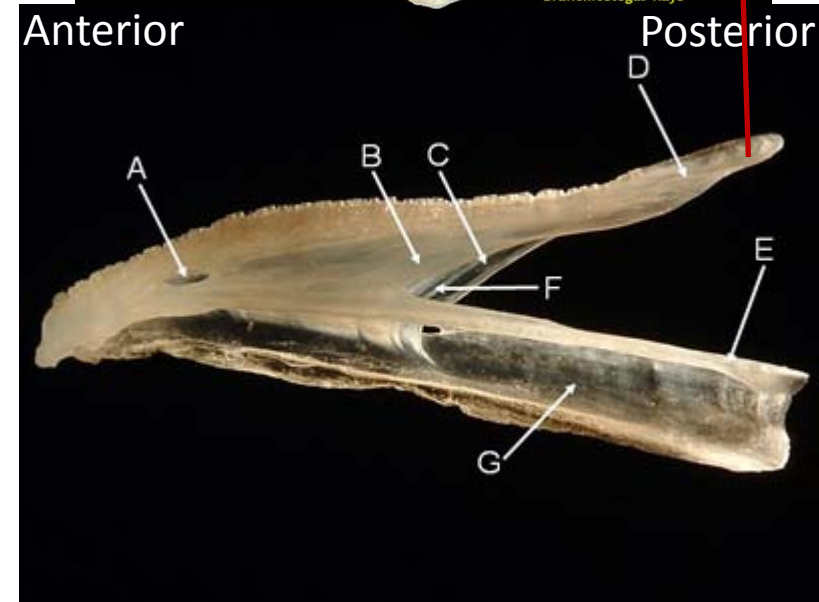
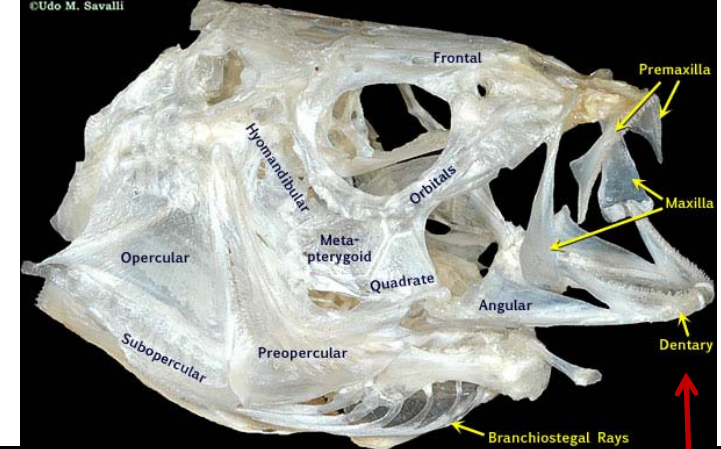
Features of the angular (from *Laemonema rhodochir*, lateral aspect).

- A = anterior process,
- B = prearticular fossa,
- C = coronoid process,
- D = quadrate facet,
- E = postarticular process,
- F = retroarticular,
- G = inferior crest.

The five main regions

2) The JAWS

- **Lower Jaw** – has an Angular articular and dentary bone
- **Dentary** - A pair of dentaries form the anterior part of the lower jaw. The teeth of the lower jaw, when present, are born on the dentary. Typically, two posterior processes, the (dorsal) coronoid process and the ventral process, articulate with the anterior process of the angular. At the anterior-most part of the lower jaw, the dentaries meet at the mandibular symphysis, which is fused in the porcupinefishes (Diodontidae).



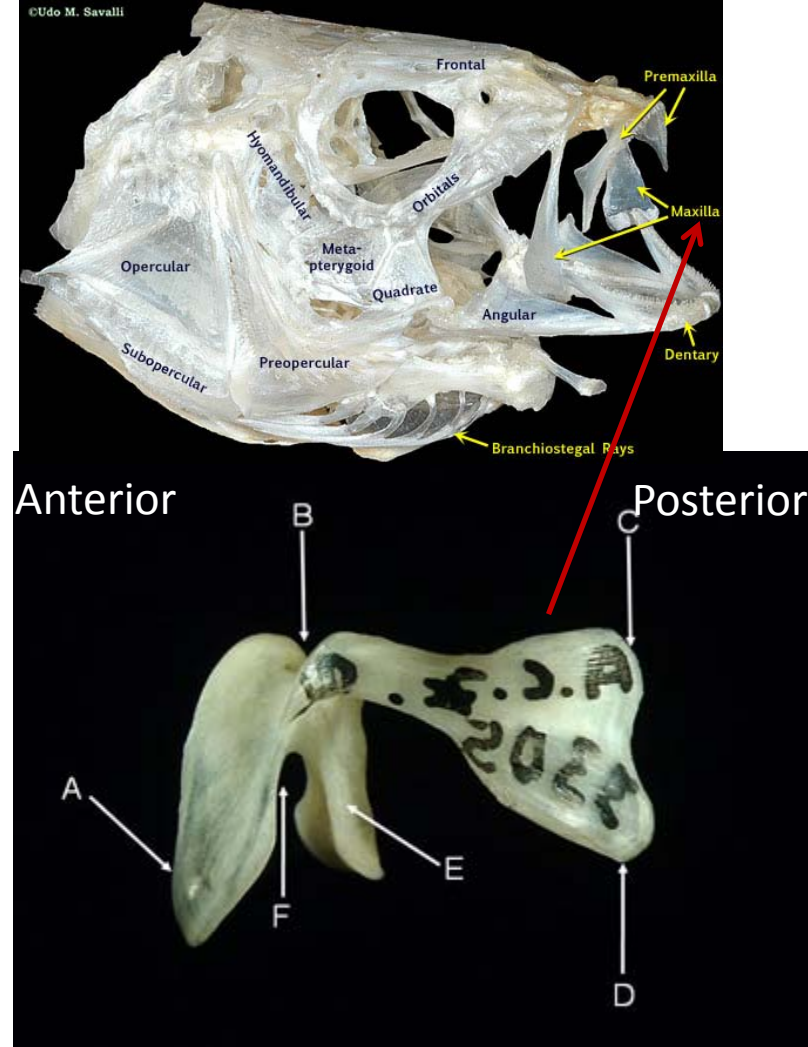
Features of the dentary (from *Laemonema rhodochir*, lateral aspect).

- A = mental foramen,
- B = external wall,
- C = internal wall,
- D = coronoid process,
- E = sensory canal,
- F = meckelian fossa,
- G = ventral process.

The five main regions

2) The JAWS

- **Upper Jaw** – has a maxilla and premaxilla (the normal teeth bearing bone)
- **Maxilla** - A pair of maxillae forms part of the upper jaw. The maxillae are located behind (in ancestral fishes) or above (in derived fishes) the premaxillae. Maxillae bear teeth in ancestral teleosts such as ladyfish (Elopidae), bonefish (Albulidae), eels (Anguilliformes), sardines (Clupeidae) and anchovies (Engraulidae). More derived teleosts tend to have toothless maxillae.



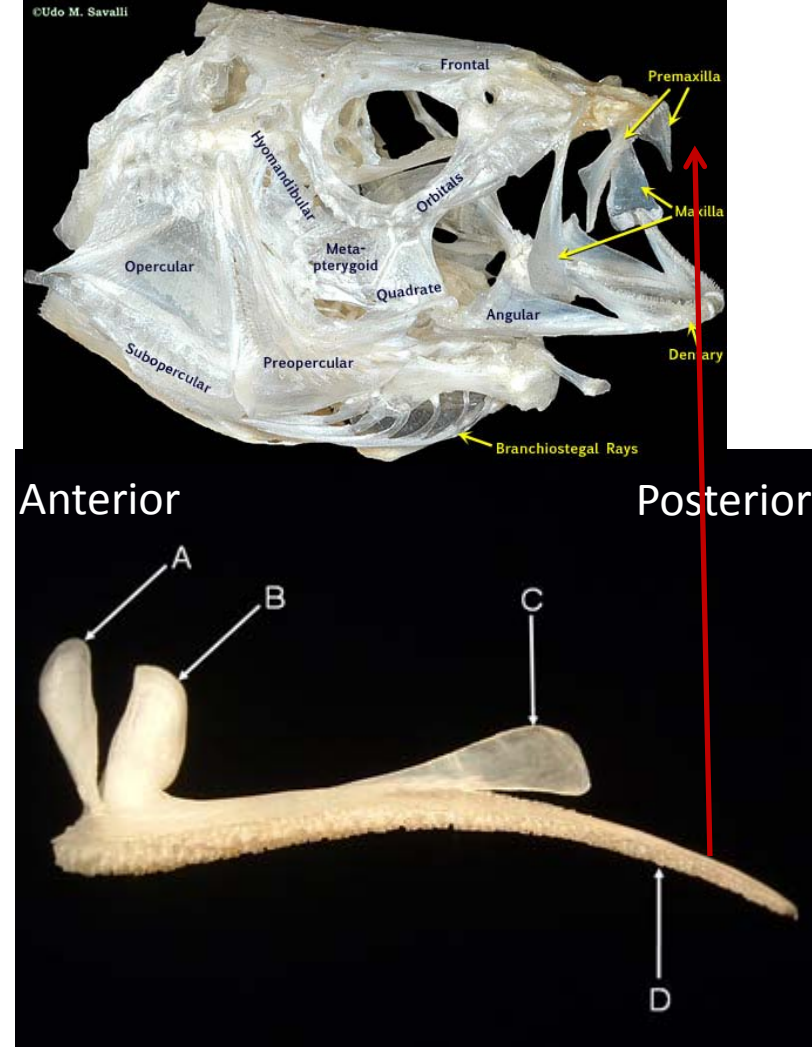
Features of the maxilla (from *Anampses cuvier*, lateral aspect).

- A = external process,
- B = palatine sulcus,
- C = maxillary process,
- D = caudal process,
- E = internal process,
- F = premaxillary sulcus.

The five main regions

2) The JAWS

- **Upper Jaw** – has a maxilla and premaxilla (the normal teeth bearing bone)
- **Premaxilla** - A pair of premaxillae forms the anterior part of the upper jaw. Both premaxillae and maxillae form the upper gape of the mouth in ancestral teleosts such as ladyfish (Elopidae), bonefish (Albulidae), eels (Anguilliformes and Saccopharyngiformes), sardines (Clupeidae) and anchovies (Engraulidae). More derived teleosts tend to have only premaxillae in the gape. The premaxillae are fused in the Diodontidae.

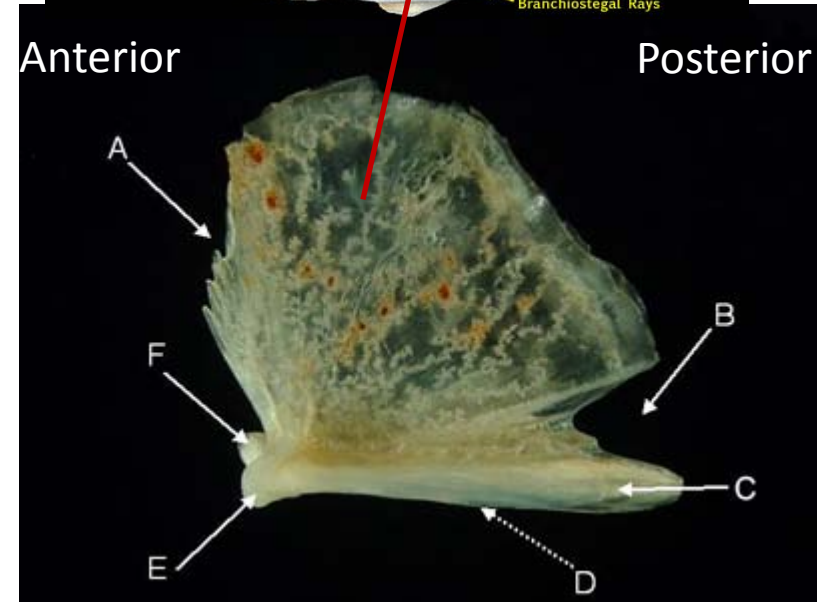
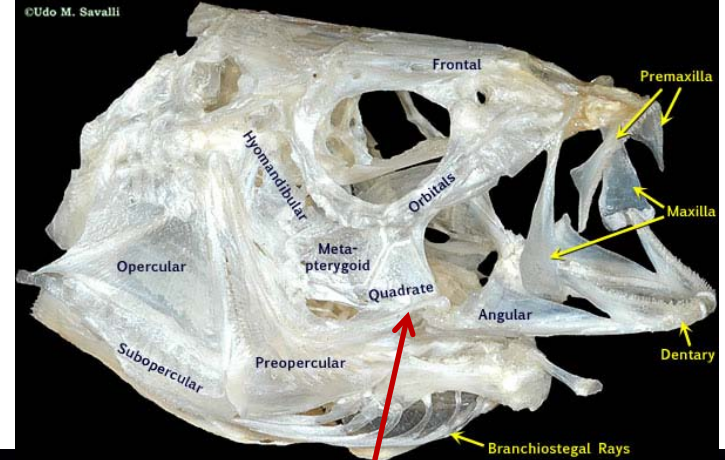


Features of the premaxilla (from *Laemonema rhodochir*, lateral aspect).
A = ascending process,
B = articular process,
C = postmaxillary process,
D = caudal process.

The five main regions

3) The CHEEKS

- **Suspensorium** – has a quadrate and hydromandibular bone
- **Quadrate** - The paired quadrates are usually triangular. The lower vertex articulates with and acts as the pivot for the angular bone of the lower jaw. A posterior, preopercular process features a groove where the preopercle articulates.

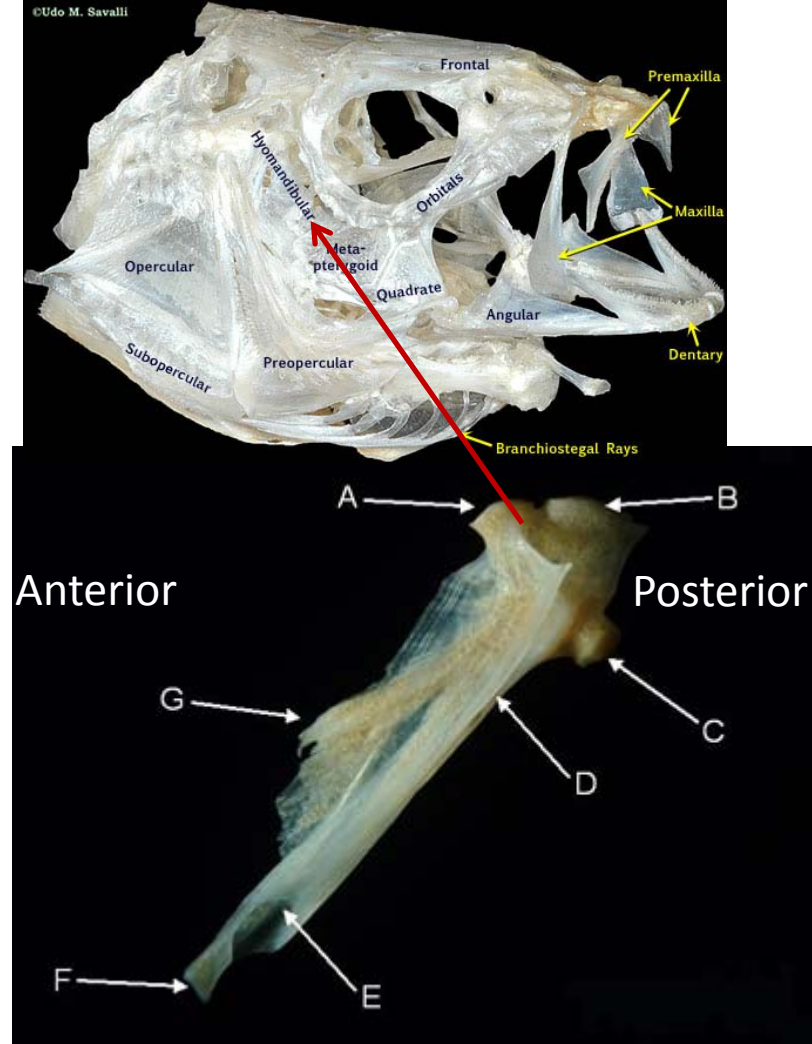


Features of the quadrate (from *Naso annulatus*, lateral aspect).
A = ectopterygoid margin,
B = symplectic incisure,
C = preopercular process,
D = preopercular groove (runs along preopercular process medial to arrow),
E = lateral condyle,
F = mesial condyle.

The five main regions

3) The CHEEKS

- **Suspensorium** – has a quadrate and hydromandibular bone
- **Hyomandibular** - The paired hyomandibulars form the upper portion of the posterior arm of the suspensorium, and are thus partly responsible for joining the jaws to the neurocranium. The dorsal part of the hyomandibular articulates with the hyomandibular fossa of the otic capsule (an excavation in the adjacent sphenotic, pterotic and prootic bones). Ventrally the hyomandibular attaches to the base of the suspensorium (quadrate) via the symplectic. A posterior process on the hyomandibular articulates with the opercle. The posterior edge of the ventral arm of the hyomandibular articulates with the preopercle. In most fishes, a hyomandibular foramen in the ventral arm allows the passage of the hyomandibular branch of the facial nerve.



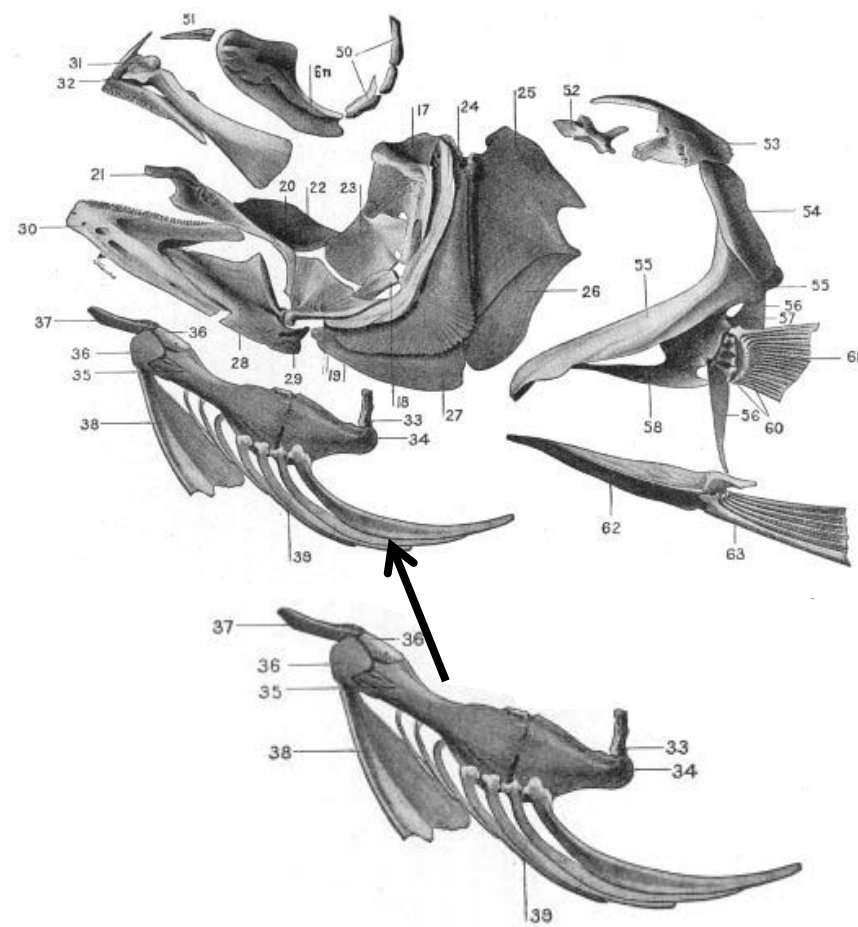
Features of the hyomandibular (from *Parupeneus pleurostigma*, lateral aspect).

- A = sphenotic facet,
- B = pterotic facet,
- C = opercular process,
- D = preopercular groove,
- E = hyomandibular foramen,
- F = symplectic facet,
- G = anterior crest.

The five main regions

4) The **HYDROID ARCH** - supports the tongue

- **Consists of the** interhyal, epihyal, ceratohyal, basihyal and glossohyal. Branchostegals ventrally attached to the epihyal.



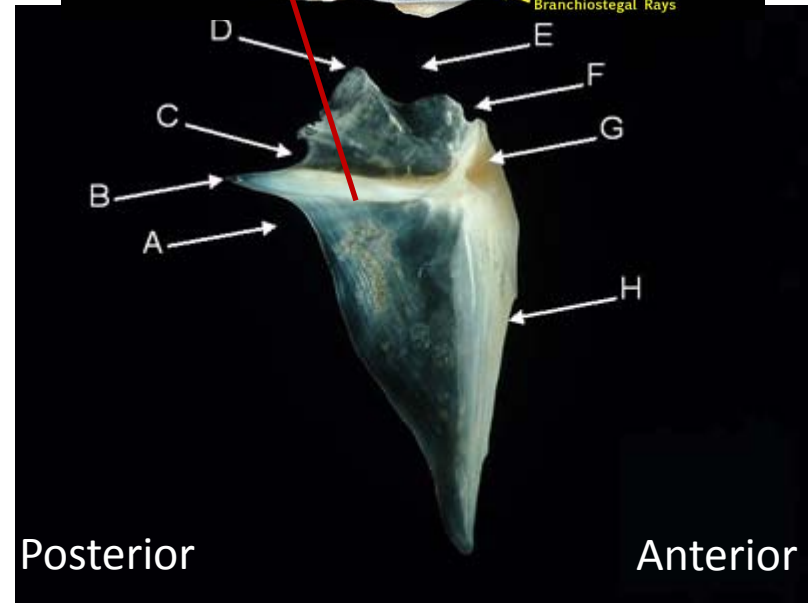
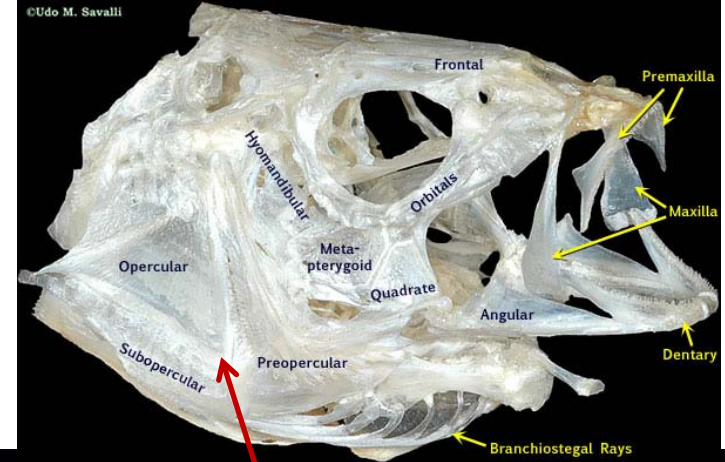
Features of the Hydroid arch (from Striped Sea-bass, *Morone saxatilis*).

33 Interhyal; 34 Epihyal; 35 Ceratohyal; 36 Basihyal; 37 Glossohyal; 38 Urohyal; 39 Branchostegals

The five main regions

5) The OPERCULA

- Consists of the operculum, preoperculum, suboperculum and the interoperculum
- Operculum - This is a paired, flat bone supporting the dorsal-most and, usually, the majority of the opercular membrane (gill cover).



Features of the opercle (from *Paurpeneus pleurostigma*, medial aspect).

A = infraspinal incisure,

B = opercular spine,

C = supraspinal incisure,

D = superior angle,

E = dorsal margin,

F = postarticular incisure,

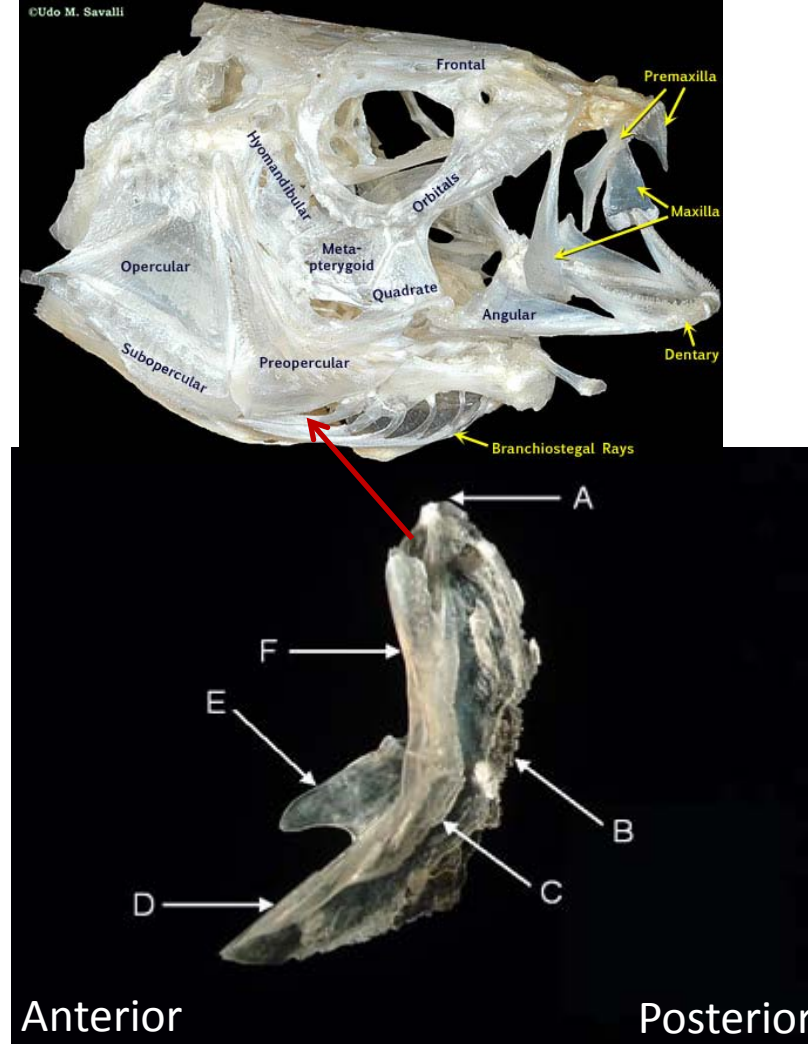
G = articular fossa,

H = anterior margin

The five main regions

5) The OPERCULA

- **Consists of the operculum, preoperculum, suboperculum and the interoperculum**
- **Preopercle** - The preopercle is a paired, chevron-shaped bone supporting part of the opercular membrane (gill flap). The preopercle carries a branch of the acoustico-lateralis system, which is housed in a sensory canal. The preopercle may also feature sensory pores. The upper arm of the preopercle articulates with and holds in place the hyomandibular. The lower arm articulates with the quadrate. The laminar, posterior wing partially covers other bones in the opercular series. The posterior border may bear stout spines (e.g., the Holocentrinae or squirrelfishes) or fine serrations.



Features of the preopercle (from *Laemonema rhodochir*, lateral aspect).

- A = upper angle,
- B = posterior wing,
- C = sensory canal,
- D = quadrate crest,
- E = anterior wing,
- F = hyomandibular crest.

- End of lecture

Lecture 9 – Jaw musculature

Jaw muscles

	<i>Originates</i>	<i>Inserts</i>	<i>Function</i>
Dilator operculi	Cranium	Operculum	Abducts operculum
Levator operculi	Cranium	Operculum	Lifts operculum -> opens jaw
Adductor operculi	Cranium	Operculum	Abducts operculum

Suspensorium muscles

	<i>Originates</i>	<i>Inserts</i>	<i>Function</i>
Levator arcus palantini	Skull	Hyomandibular	Increases buccal volume
Adductor arcus palantini	Parasphenoid	Hyomandiular	Decreases buccal volume

Opercular muscles

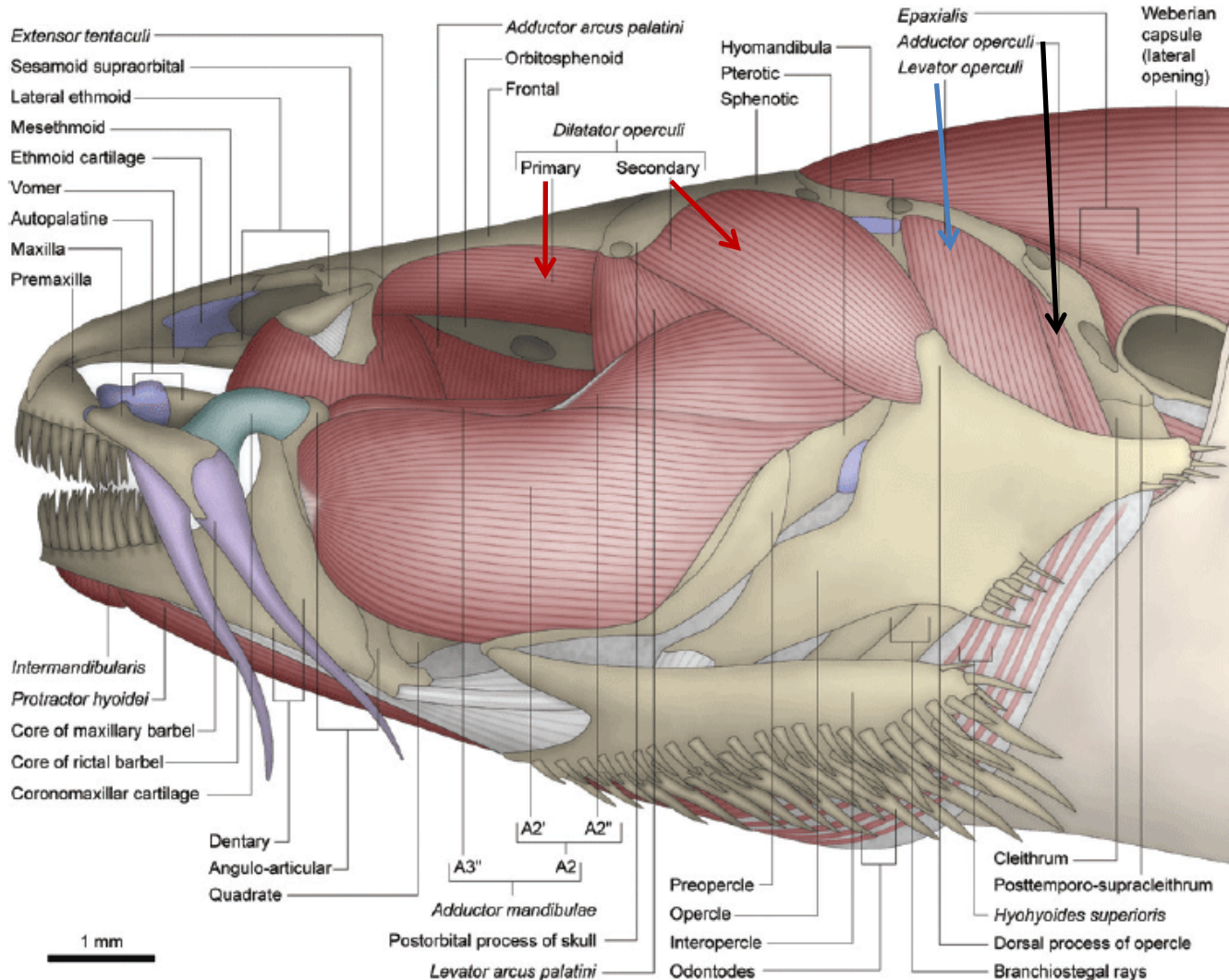
	<i>Originates</i>	<i>Inserts</i>	<i>Function</i>
Adductor mandibulae I	Suspensorium	Maxilla	Holds maxilla in place during feeding. Closes jaw
Adductor mandibulae II	Suspensorium	Post. Dentary via ligament	Closes mouth and assists adducting suspensorium
Adductor mandibulae II	Suspensorium	Dentary and maxilla	Closes mouth and assists adducting suspensorium

Adduction - A motion that pulls a structure or part *towards* the midline of the body.

Abduction - A motion that pulls a structure or part *away from* the midline of the body.

JAW MUSCLES

	<i>Originates</i>	<i>Inserts</i>	<i>Function</i>
Dilator operculi	Cranium	Operculum	Abducts operculum
Levator operculi	Cranium	Operculum	Lifts operculum -> opens jaw
Adductor operculi	Cranium	Operculum	Adducts operculum



Adduction - A motion that pulls a structure or part towards the midline of the body.
Abduction - A motion that pulls a structure or part away from the midline of the body.

Fig. 7. Left lateral view of head of *Trichogenes longipinnis* (Trichogeninae), LIRP 1059 (75.5 mm SL). Antorbital and core of nasal barbels removed.

Suspensorium muscles

	<i>Originates</i>	<i>Inserts</i>	<i>Function</i>
Levator arcus palantini	Skull	Hyomandibular	Increases buccal volume
Adductor arcus palantini	Parasphenoid	Hyomandibular	Decreases buccal volume

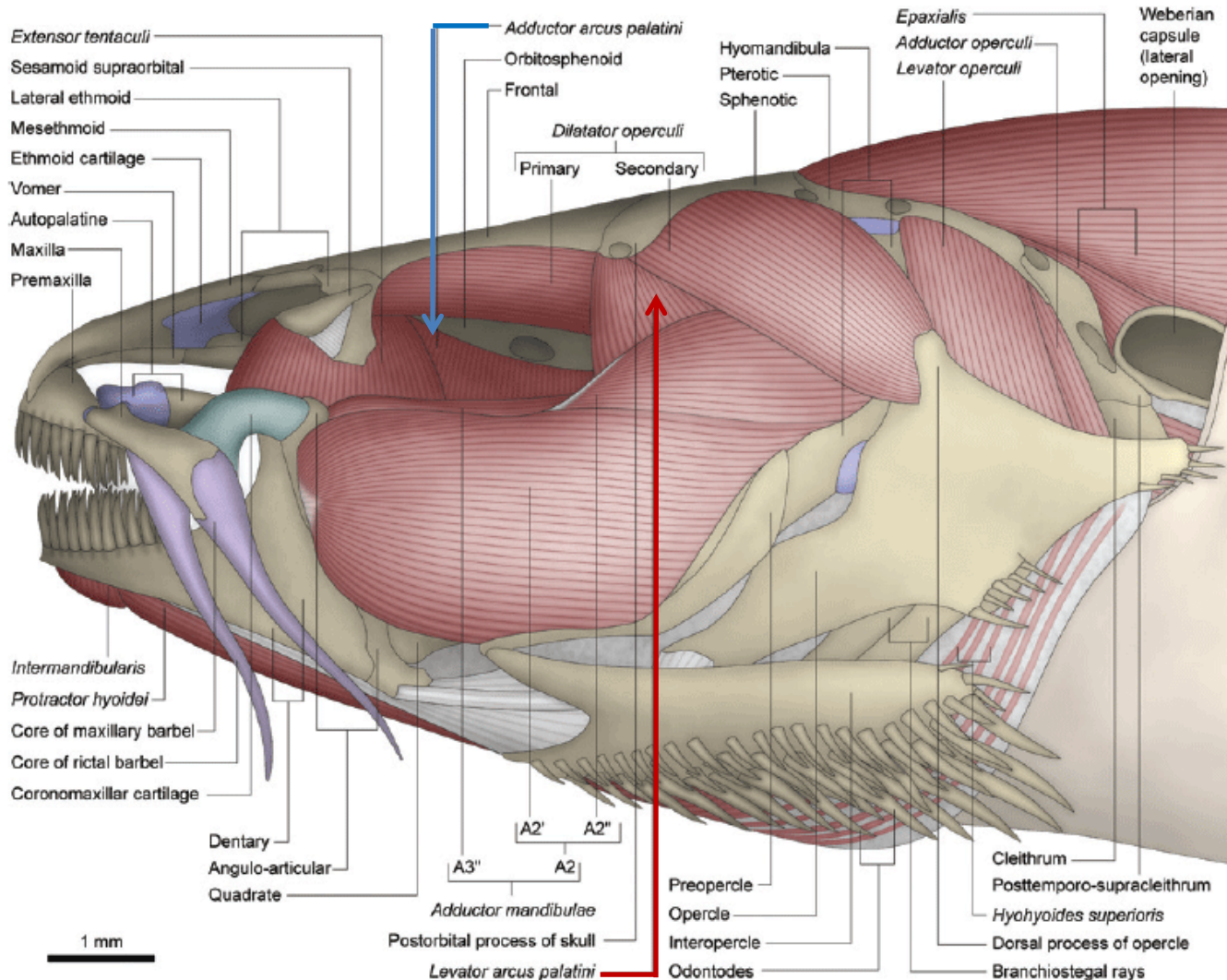
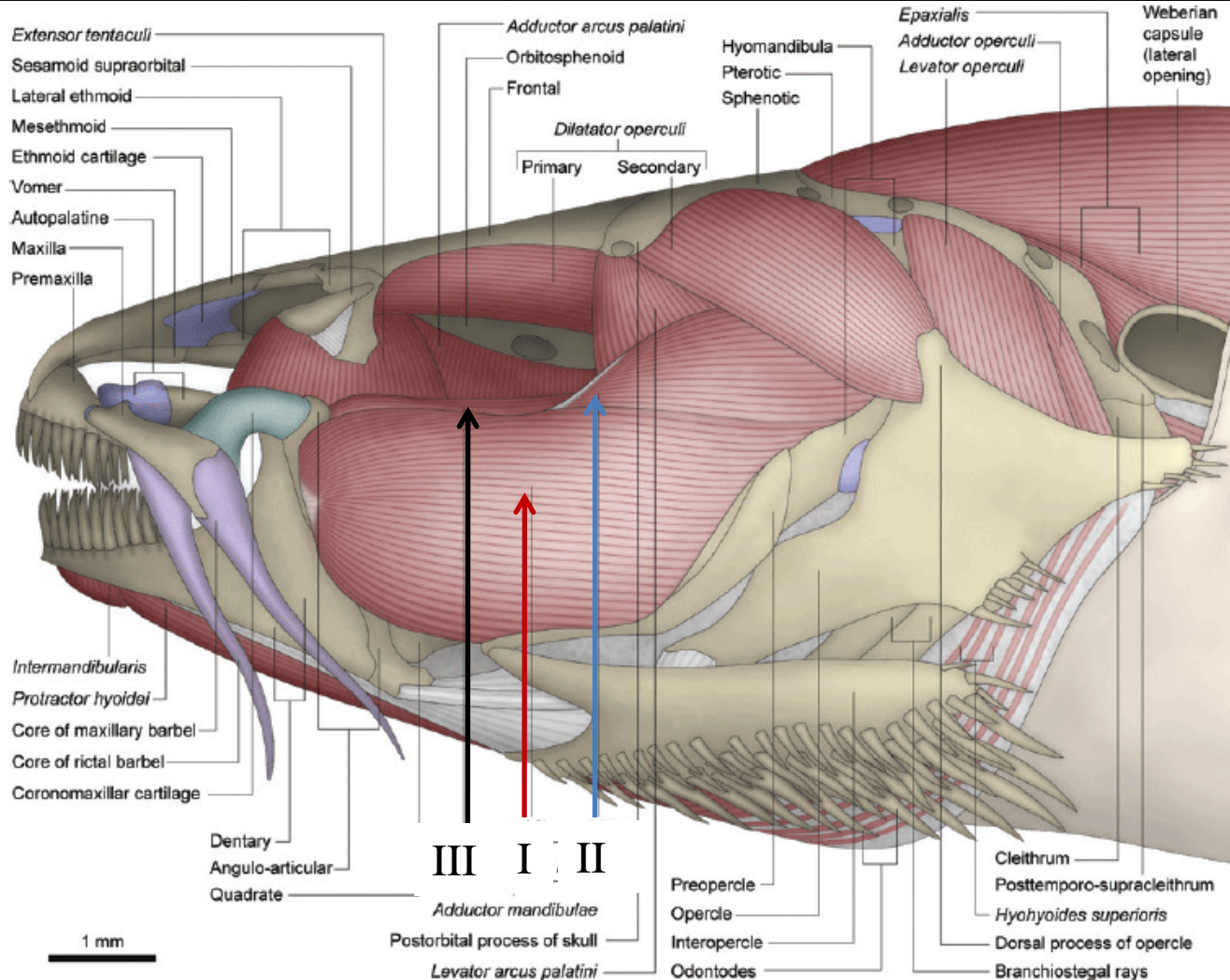


Fig. 7. Left lateral view of head of *Trichogenes longipinnis* (Trichogeninae), LIRP 1059 (75.5 mm SL). Antorbital and core of nasal barbels removed.

Adduction - A motion that pulls a structure or part towards the midline of the body.
Abduction - A motion that pulls a structure or part away from the midline of the body.

Opercular muscles	<i>Originates</i>	<i>Inserts</i>	<i>Function</i>
Adductor mandibulae I	Suspensorium	Maxilla	Holds maxilla in place during feeding. Closes jaw
Adductor mandibulae II	Suspensorium	Post. Dentary via ligament	Closes mouth and assists adducting suspensorium
Adductor mandibulae III	Suspensorium	Dentary and maxilla	Closes mouth and assists adducting suspensorium



Adduction - A motion that pulls a structure or part towards the midline of the body.
Abduction - A motion that pulls a structure or part away from the midline of the body.

Datovo & Bockmann (2010)

overhead

Fig. 7. Left lateral view of head of *Trichogenes longipinnis* (Trichogeninae), LIRP 1059 (75.5 mm SL). Antorbital and core of rictal barbel removed.

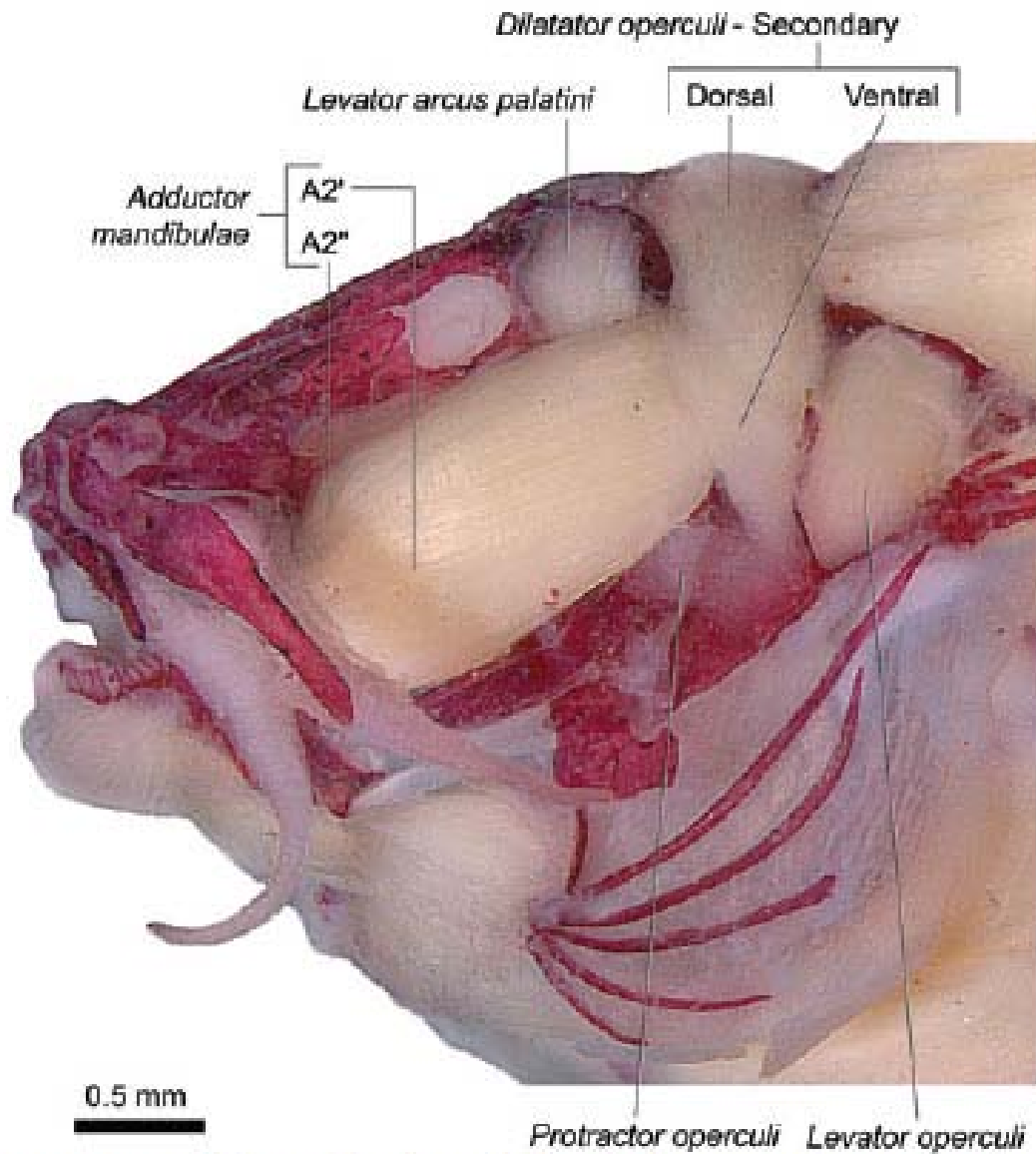


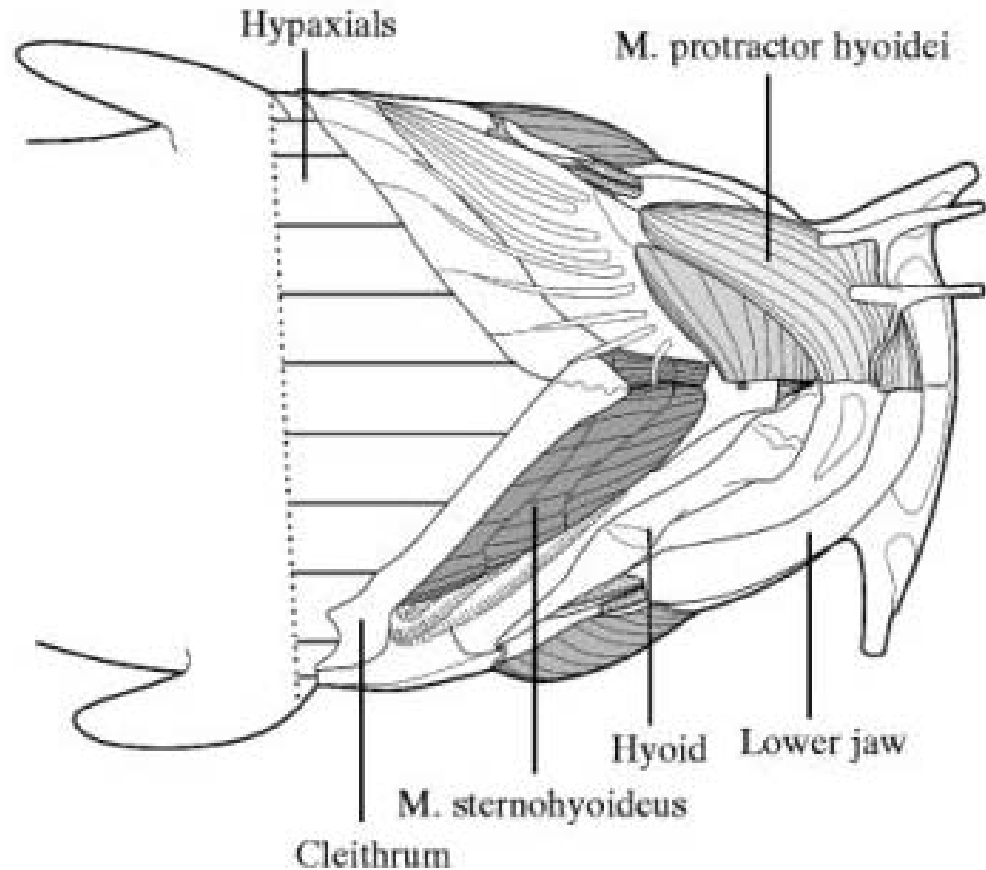
Fig. 15. Left lateral view of head of *Sarcoglanis simplex* (Sarcoglanidinae), LIRP 7437 (16.9 mm SL). Antorbital and sesamoid supraorbital bone removed.

Ventral head muscles (overhead)

- Intermandibulars
- Protractor hyoidei
- Ceratohyal
- Hyohyoideus inferior
- Hyohyoidei abductores
- Hyohyoidei adductores
- Sternohyoideus

(A) Lateral view of the head of a juvenile *Clarias gariepinus*

Ventral view on the hyoid musculature of the same juvenile *Clarias gariepinus*. Note that the bottom of the fish has been dissected to expose the lower jaw, hyoid, cleithrum and m. sternohyoideus. Scale bar, 5 mm.

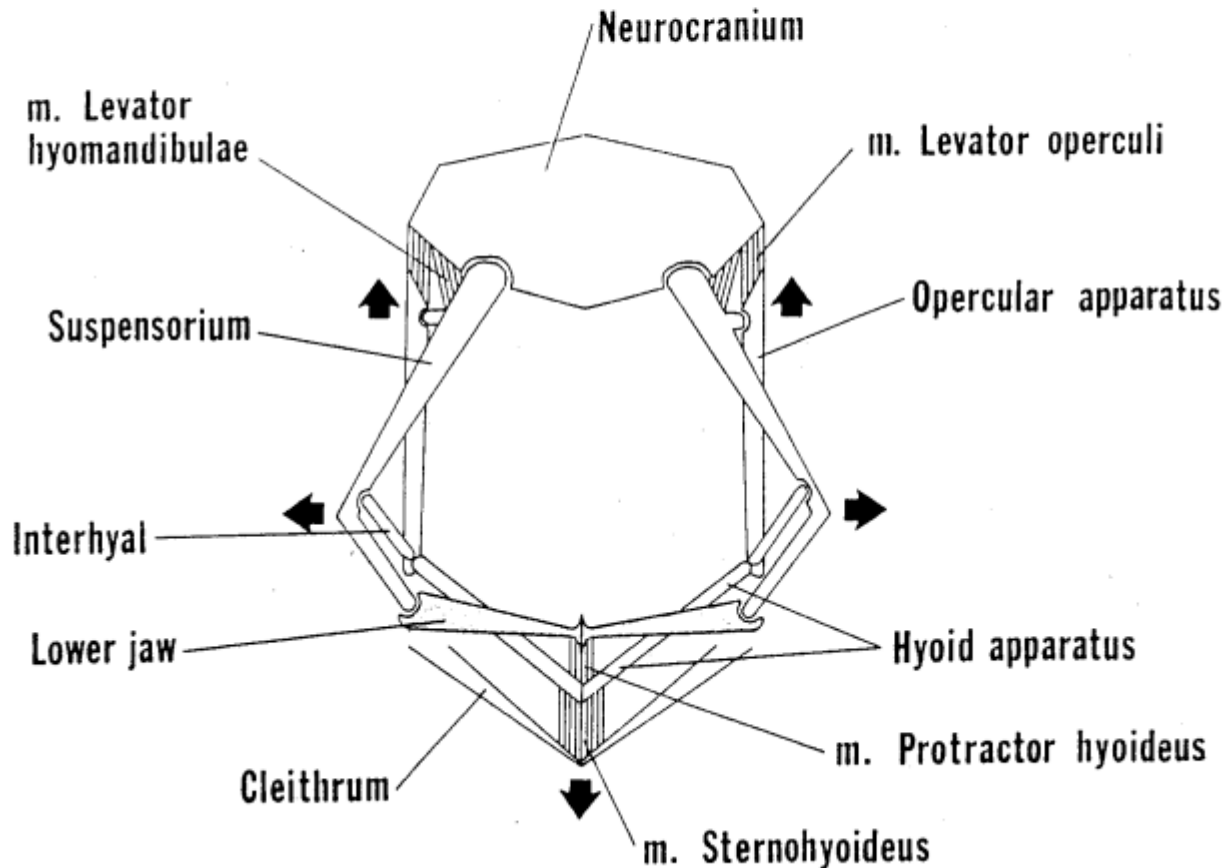


Herrel, A. et al. J Exp Biol 2005;208:2091-2102

Jaw opening and closing mechanism

1. GAPE AND SUCK FEEDING.

Generally speaking, the vast majority of living fishes are **gape and suck feeders**. They feed by opening the mouth while simultaneously lowering the floor of the mouth and expanding the sides of the mouth cavity. This great and sudden increase in volume creates **negative pressure** (i.e., a vacuum), which, in turn, results in a sudden rush of water into the mouth. When directed adequately by the predator, it's this sudden rush of water that carries or pulls prey into the mouth to be swallowed.



tiger fish.htm



freshwater eel.htm



Stonefish.htm

When the jaws are closed, the water and whatever it contains stays in the expanded **oral cavity**; water and hopefully prey do not pass out through the mouth. A pair of membranous valves just inside the upper and lower jaws (present in most fishes) helps prevent water from escaping anteriorly. These are called “**oral valves.**”

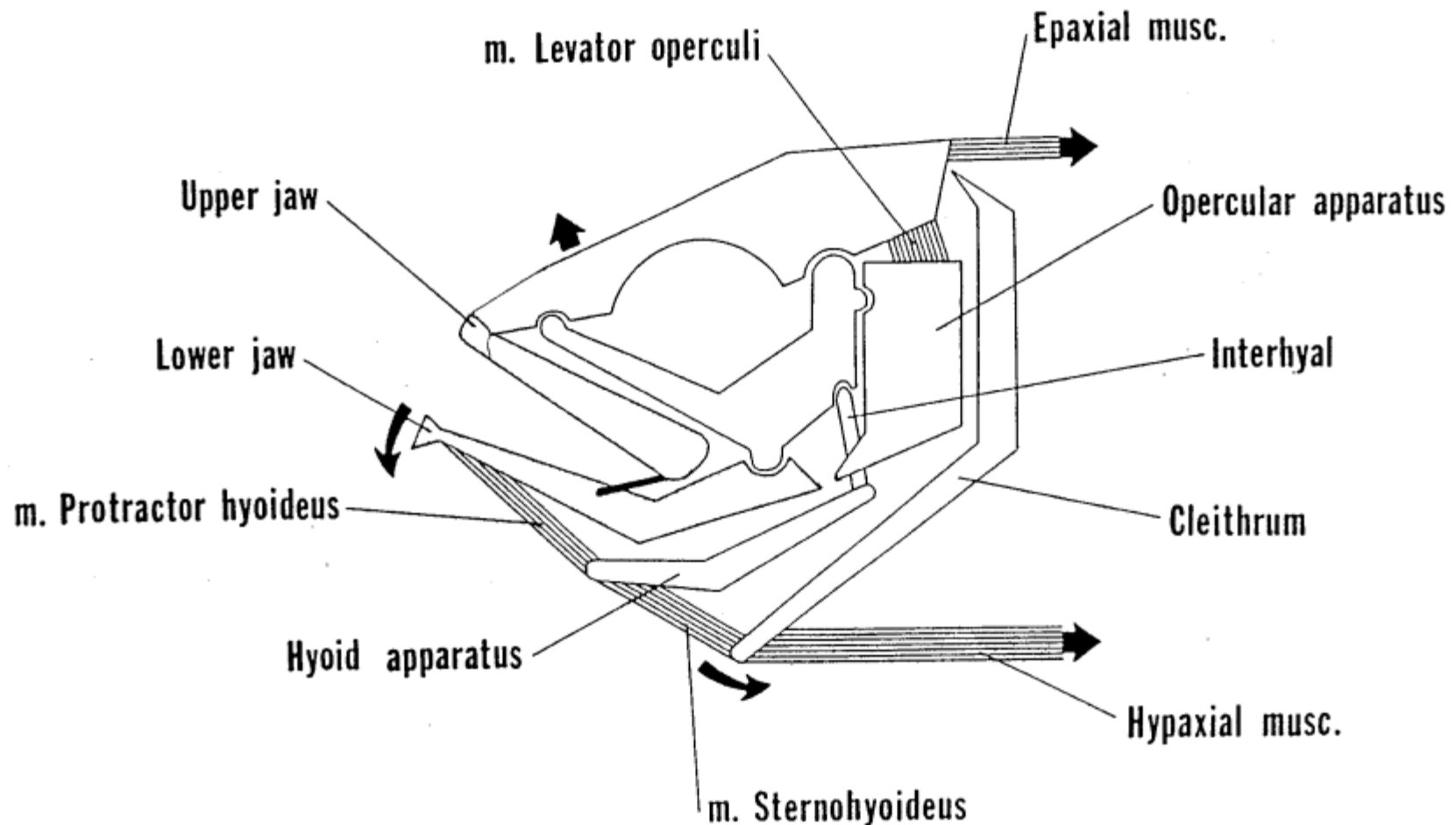
Once the jaws are closed, the floor of the throat is raised and the cheeks or sides of the mouth are contracted, forcing the trapped water out through the **gills**. Any food item contained in the water is strained out by the gills, particularly the **gill rakers**, and passed back into the opening of the esophagus to be swallowed.

All of these various movements of the jaws and the mouth cavity are made possible by a complex series of **interlocking bones**, and **tendons** and **muscles** attached to them. The complexity is increased by the fact that there is often more than one way to accomplish essentially the same movement. So let's look in some detail at how fishes open their mouths.

Mouth opening in primitive fishes

2. THE HYOID COUPLING OF PRIMITIVE ACTINOPTERYGIAN FISHES.

In primitive actinopterygians, i.e., living sturgeons, paddlefishes, and even in gars, the lowering of the mandible or opening the mouth seems to be entirely dependent on lowering the floor of the throat. These primitive forms have only one means by which they can open the mouth, a **biomechanical coupling** called the **hyoid coupling**.



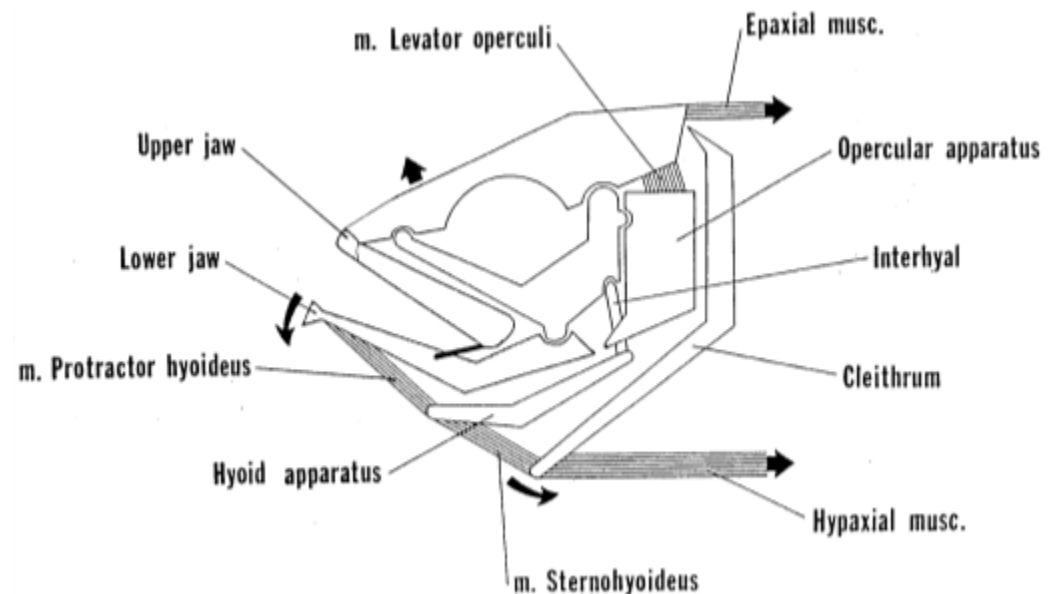
Lower jaw depression is initiated by contractions of body musculature, the **epaxial musculature** above and the **hypaxial musculature** below. Contraction of the epaxial musculature, which inserts on the rear of the cranium, causes the head to rotate upward relative to the body axis. Contraction of the hypaxial musculature, a large part of which inserts on the cleithrum, causes a backward and downward rotation of the **pectoral girdle**.

Anteriorly, the **cleithra**, one on each side, are attached to the **hyoid apparatus** by a strong muscle called the **sternohyoideus**—this muscle contracts as well so that the backward and downward movement is transmitted to the hyoid. Finally, because the **hyoid** lies between, and is attached to, the elements of the lower jaw by skin and ligaments, the downward and backward pull on the hyoid apparatus is transmitted to the **lower jaw**.

This mechanism is then an **indirect way** of opening the mouth. Any opening of the mouth is preceded by a downward and backward movement of the floor of the mouth. This results in an expansion of the **oral cavity**, which in turn, creates suction—water is drawn into the mouth as the lower jaw is depressed.



Paddlefish.htm



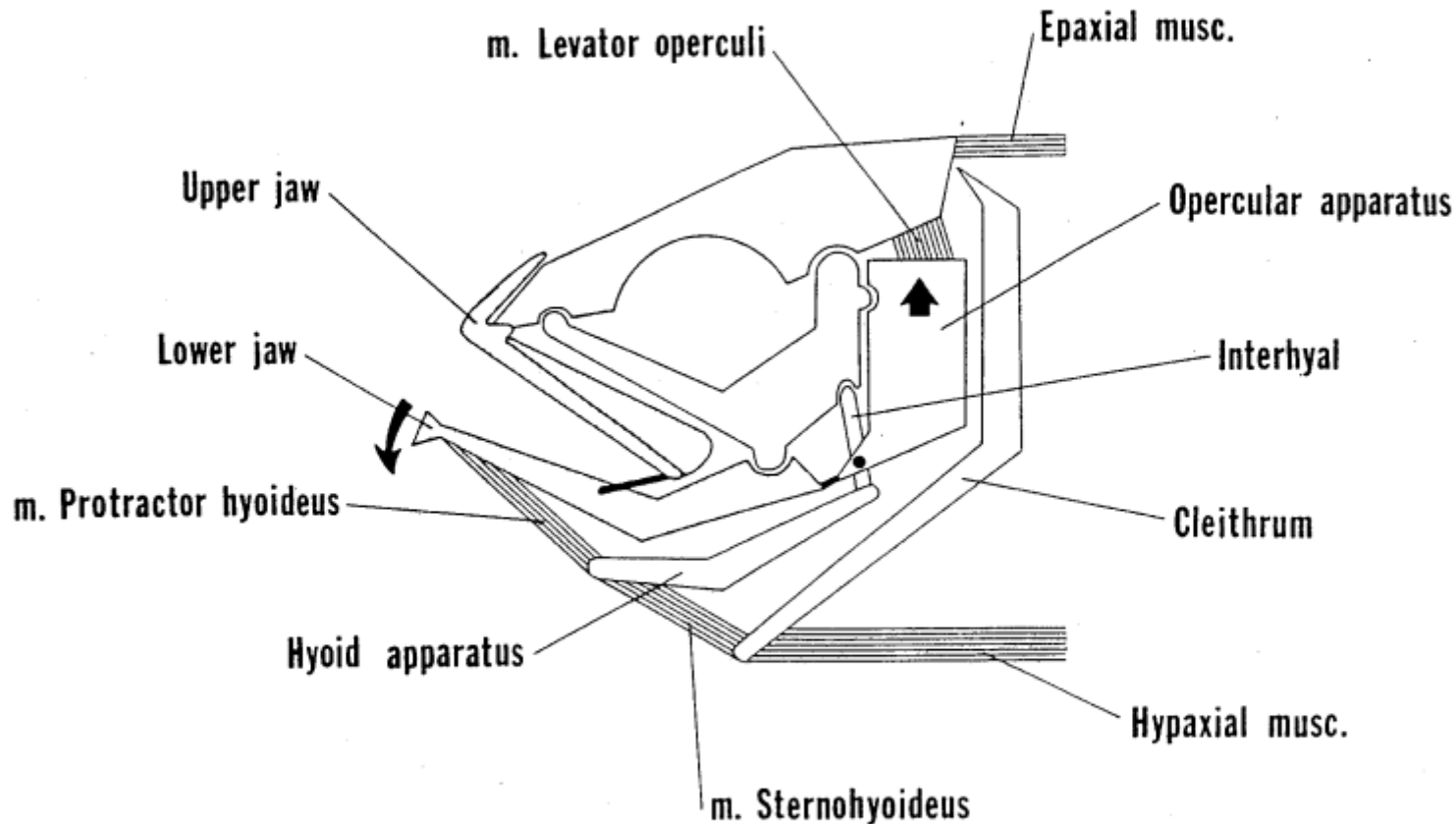
This is simply a **primitive gape and suck feeding mechanism** found today in living sturgeons, paddlefishes, and gars. And, as you know, most fishes rely on this creation of negative pressure inside the mouth cavity to pull prey and the water that surrounds it into the mouth. The effectiveness of the suction in capturing prey depends on two things:

1. **The degree to which the mouth cavity can be expanded**
2. **The suddenness with which the mouth cavity can be expanded**



3. THE OPERCULAR COUPLING OF DERIVED ACTINOPTERYGIANS.

O.K., we've described the biomechanical coupling responsible for opening the mouth in **primitive actinopterygians**. What about **derived actinopterygians**? It turns out that the bowfin (genus *Amia*) and teleosts have developed a second, more-or-less independent system for opening the mouth that supplements the coupling just described for primitive actinopterygians, called the **opercular coupling**.

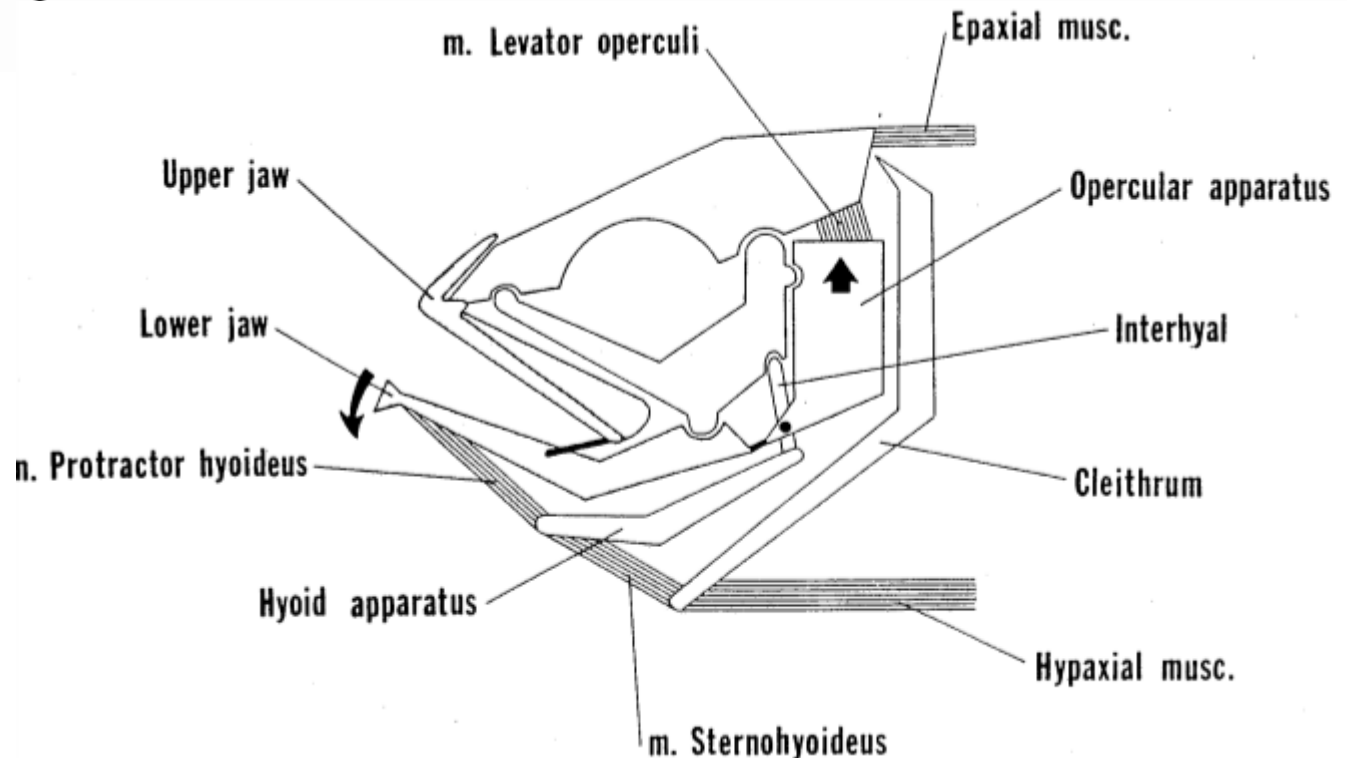


Opening of the mouth with the **opercular coupling** is initiated by contraction of the **levator operculi**, a muscle that originates on the **cranium** and inserts along the dorsal margin of the **opercle**. This causes the opercle to swing up and backward. Since the **subopercle** and **interopercle** are attached to the opercle, this movement is transmitted ventrally throughout all the elements of the **opercular apparatus**. In turn, the interopercle pulls back on the lower jaw by means of a strong ligament that has developed between these two bones.

Mouth opening in more derived fishes

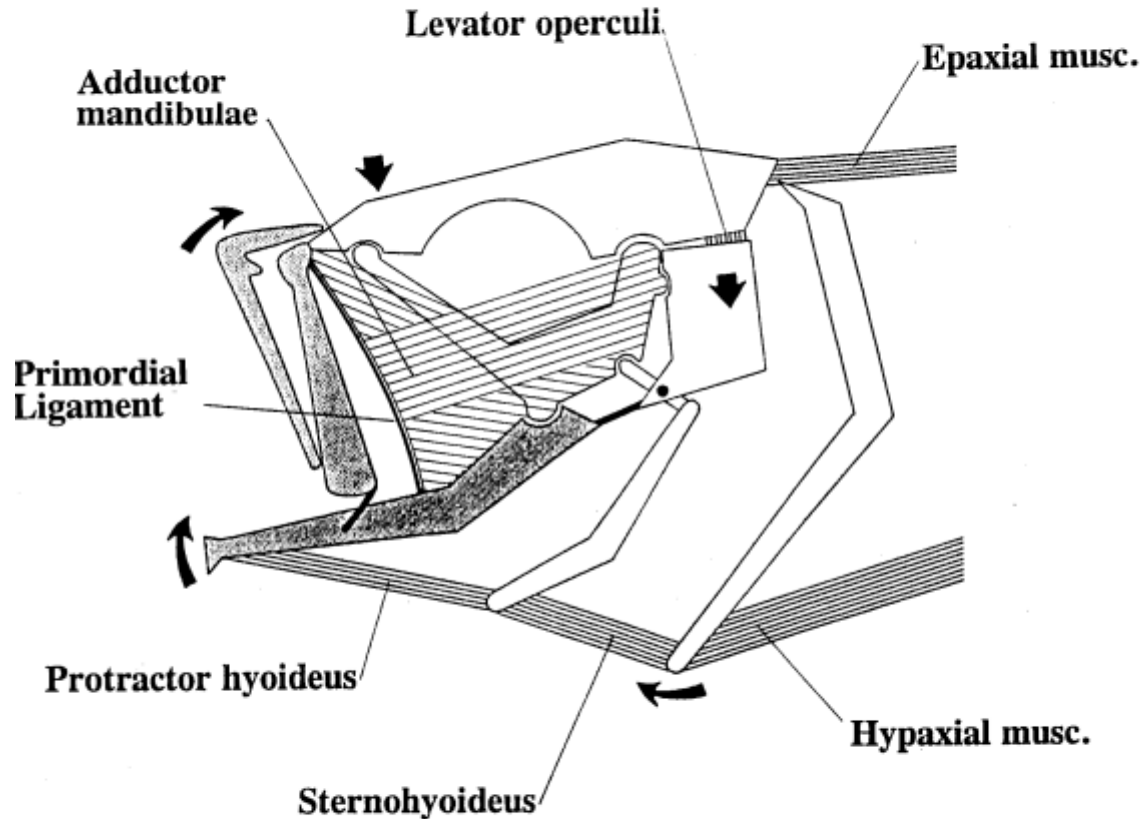
So, in addition to the **indirect hyoid coupling** inherited from primitive actinopterygians, the bowfin and teleosts have evolved a second, more-or-less independent and **direct mechanism** for opening the mouth, one that does not involve the creation of suction.

What good is it? Because this new **opercular coupling** does not involve the creation of negative pressure, i.e., suction, its development was a necessary pre-adaptation for those kinds of fishes that browse along nipping at rocks and coral, picking up small prey from soft bottoms, forms that bite off and crush chunks of coral—fishes like surgeonfishes, parrotfishes, wrasses, triggerfishes, and a whole host of other perciform taxa.



4. CLOSING THE MOUTH.

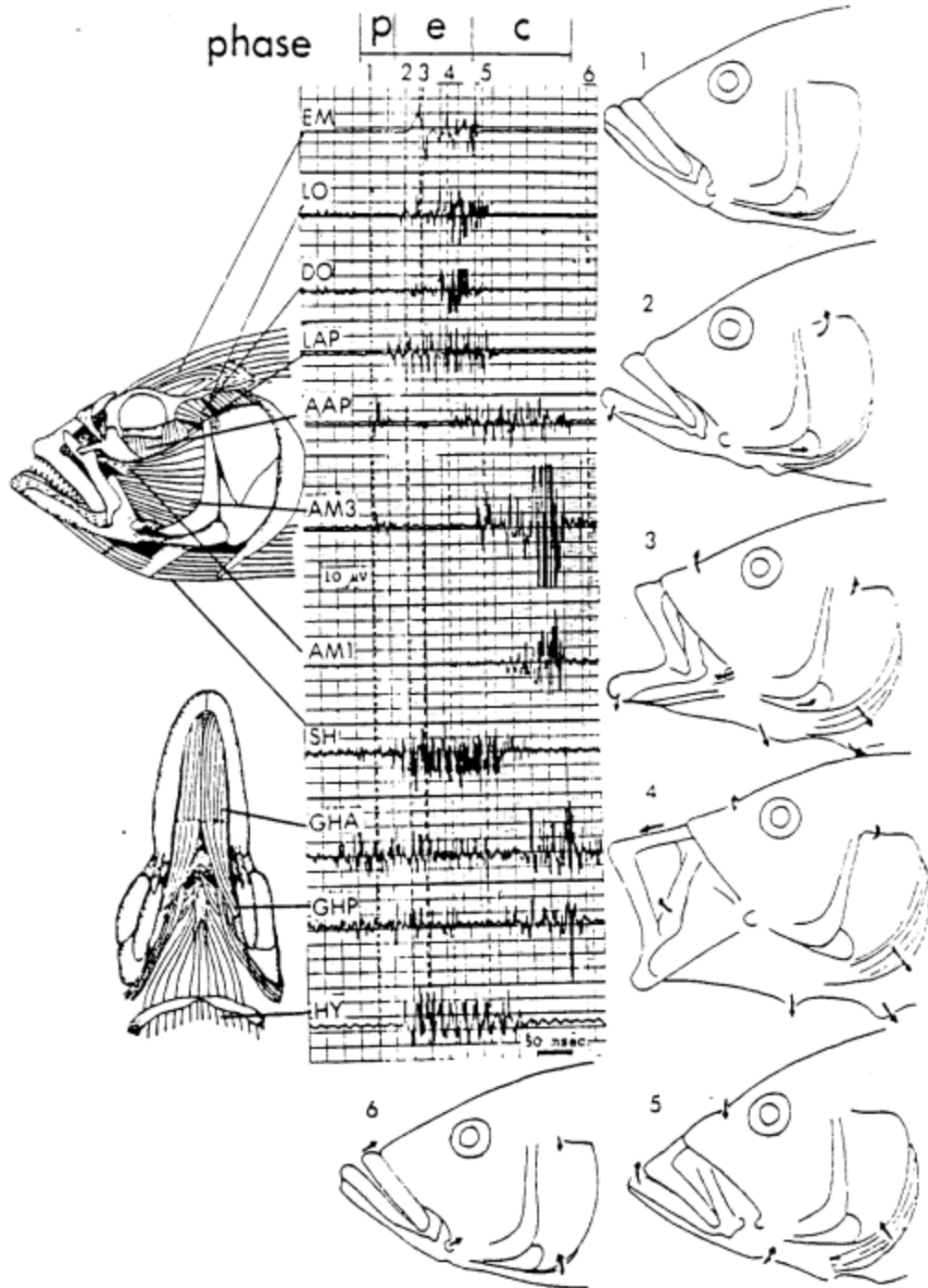
Getting the mouth closed is relatively simple. It is accomplished by contraction of a large complex muscle called the **adductor mandibulae** (cheek muscles), which is usually divided into three or four separate sections. It originates on the bones of the **suspensorium** and has a complex insertion primarily along the length of a long ligament that stretches between the head of the maxilla and the inner surface of the lower jaw. This ligament is called the **primordial ligament**.



The **adductor mandibulae** is a very important muscle because all movement related to feeding (whether it be full gape and suck or simple nipping, grasping, or crushing) as well as respiration depends on it.

The size and shape of the **adductor mandibulae** varies greatly among teleosts and it is a widely used character complex in systematic studies, especially in comparing higher taxonomic categories.

Epaxial
 Levator operculi
 Dilatator operculi
 Levator arcus palatini
 Adductor arcus palatini
 Adductor mandibulae III
 Adductor mandibulae I
 Sternohyoideus
 Hyoideus abductor
 Hyoideus adductor
 Hypaxial



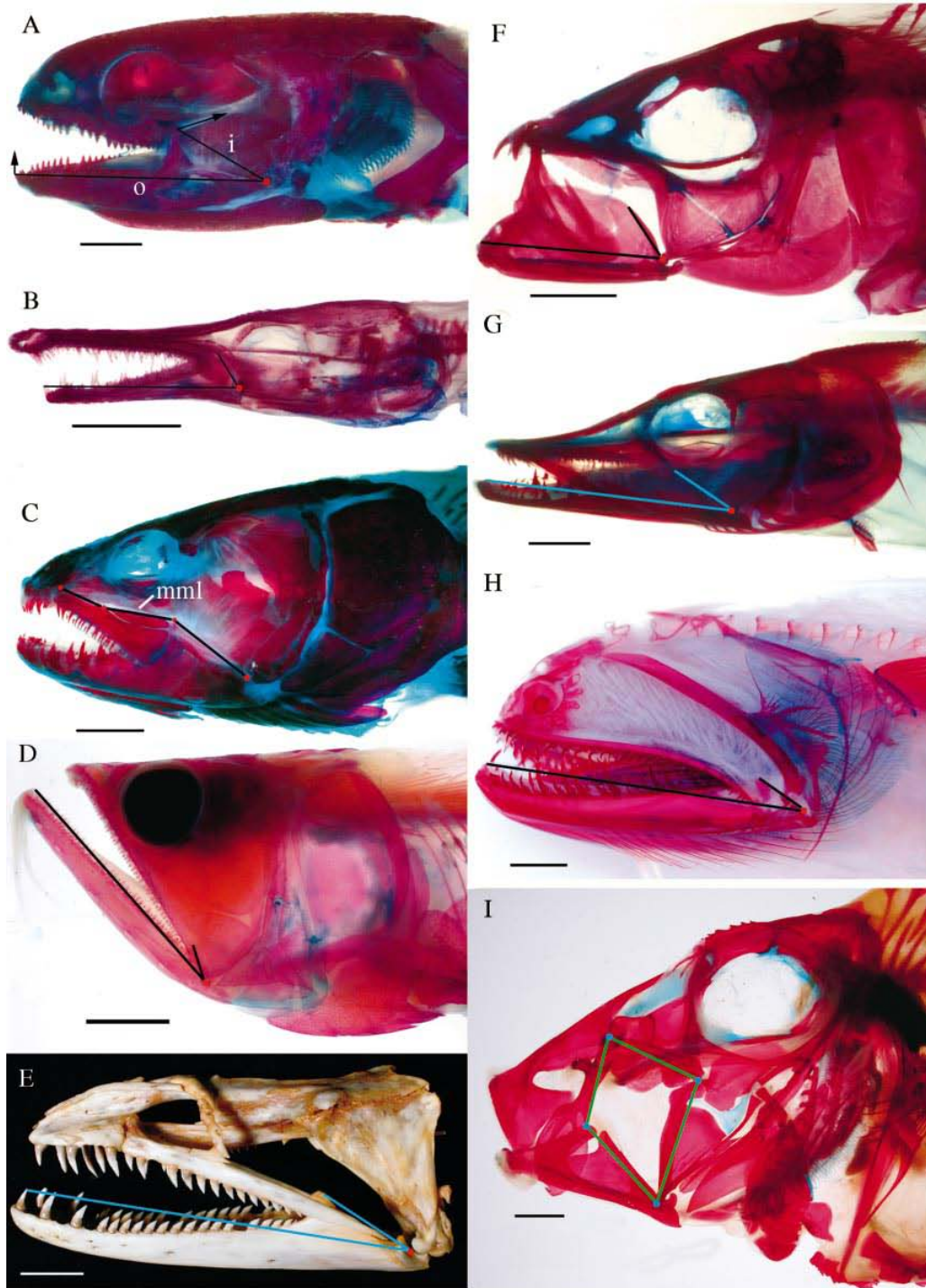
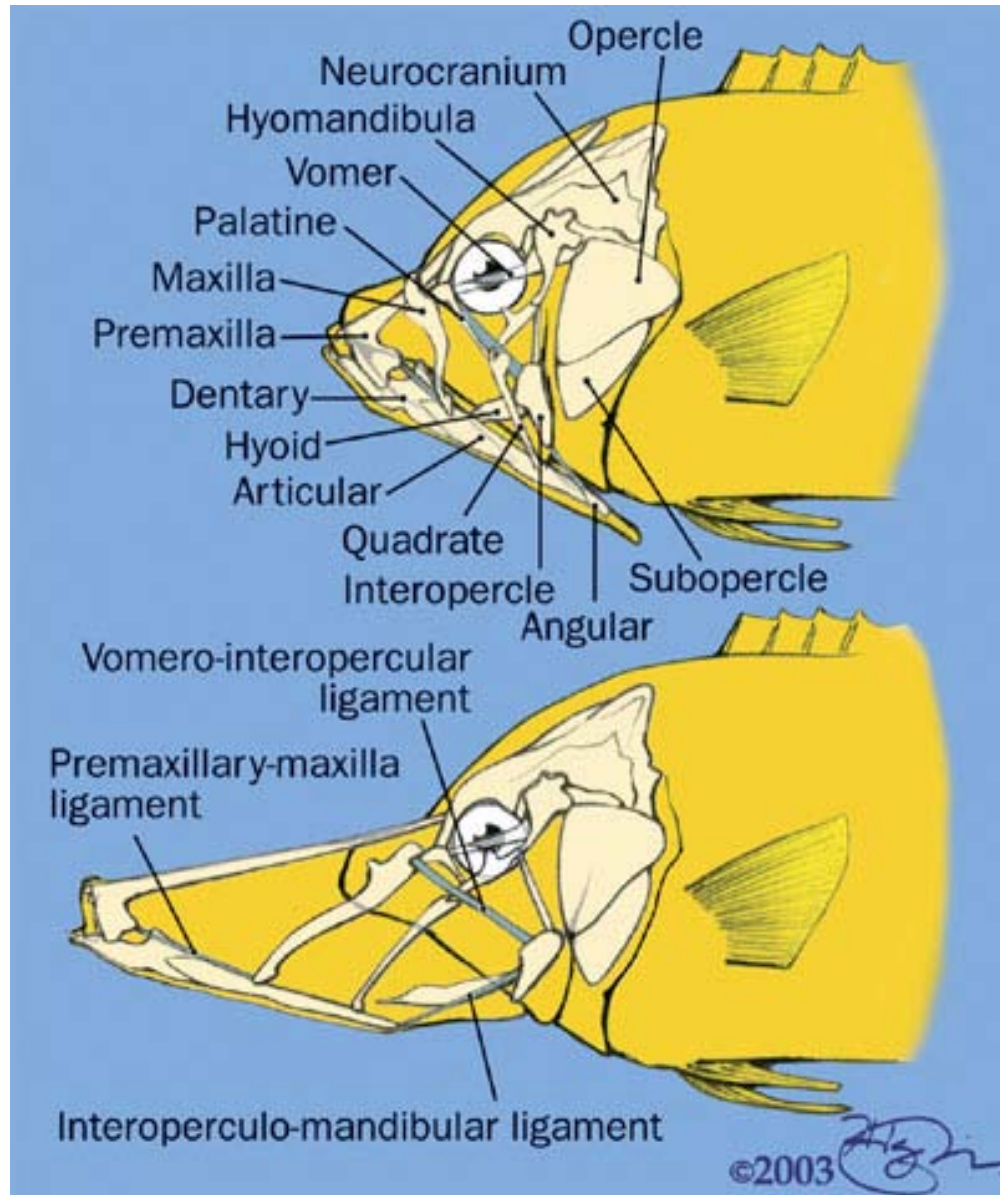


FIG. 4. Skull diversity, mandibular lever variation, and linkage structure in actinopterygian fishes. (A) The bichir, *Polypterus senegalus*, illustrating a simple mandibular lever with input (i) and output (o) lever arms. (B) Lever dimensions of the alligator gar *Atractosteus spatula*. (C) The bowfin, *Amia calva*, illustrating the 3 movable elements in the four-bar linkage for maxillary rotation; mml, maxillomandibular ligament. (D) Lever dimensions of the arawana, *Osteoglossum bicirrhosum*. (E) Lever dimensions of the moray eel, *Gymnothorax javanicus*. (F) Lever dimensions of the clupeid *Sardinella aurita*. (G) Lever dimensions of the northern pike, *Esox lucius*. (H) Lever dimensions of the bombay-duck, *Harpadon nehereus*. The earliest clade to show an anterior jaws four-bar linkage with a rotational palatine that powers protrusion is the dorids illustrated by (I) the rosy dory, *Cyttopsis rosea*. Scale bar 5 mm. WESTNEAT (2004)

An extreme example: the slingjaw wrasse



Wrasse.htm



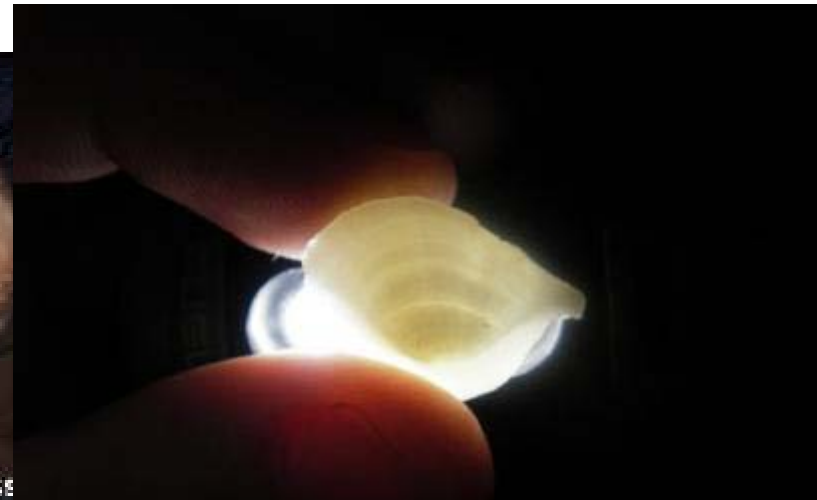
Lecture 11 – Otolith structure (Rosin and Mcgarry)

What is an otolith?

Otoliths, or "earstones", are found in the head of all fishes other than sharks, rays and lampreys.

An otolith is composed of a small proportion of organic matter (10-20%).

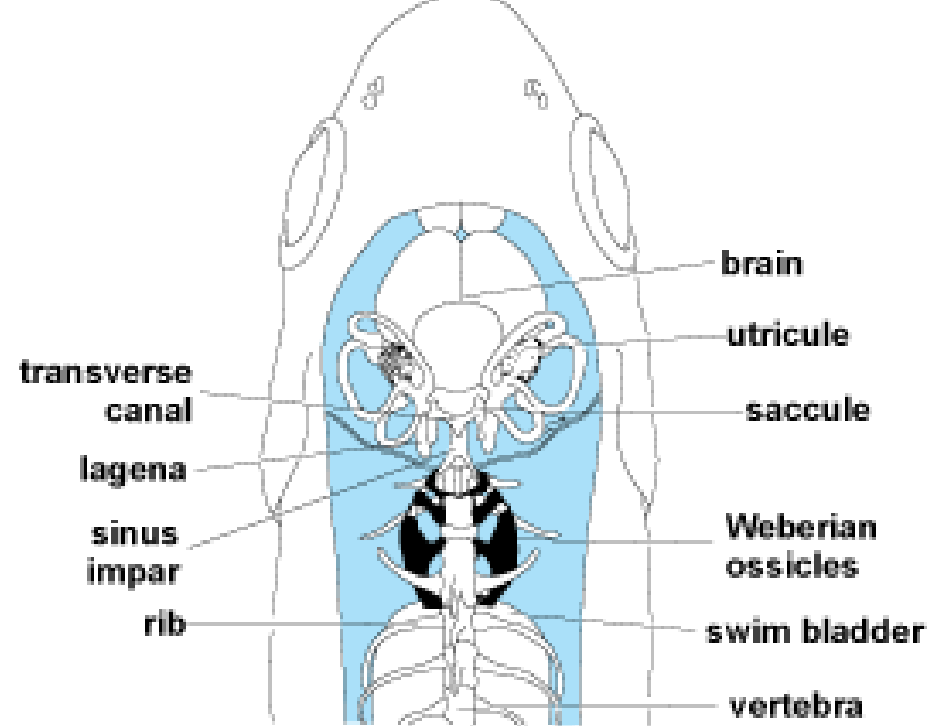
The rest consists of a fibrous protein known as otolin. The chemical structure of otolin is very similar to keratin.



- A bony fish's inner ear consists of 3 otolith pairs that are cased in “sacks” which are the swellings of three semicircular canals, arranged in three planes.
- The sack are lined with neuromasts, which sense the movements of the otoliths.
- The three otolith pair are known as the sagittal, asteriscal and lapillar



- The Sagitta is generally the largest of the three and is encased in the sacculus , which lies in the cranial cavity of the brain case.
- The sacculus is in the pars inferior region of the inner ear and the Asteriscus (the smaller earstone), which is encased in the Lagena.
- The lappilus, is enclosed in the Utriculus is connected by three semicircular canals, which are found in the pars superior region of the inner ear.
- Sharks do not have otoliths, but juveniles have endolymphatic ducts (which open into pores on the head).
- These ducts allow mineral crystals or grains of sand to enter the three sacs in the inner ear. These grains act as otoliths to help detect gravity.

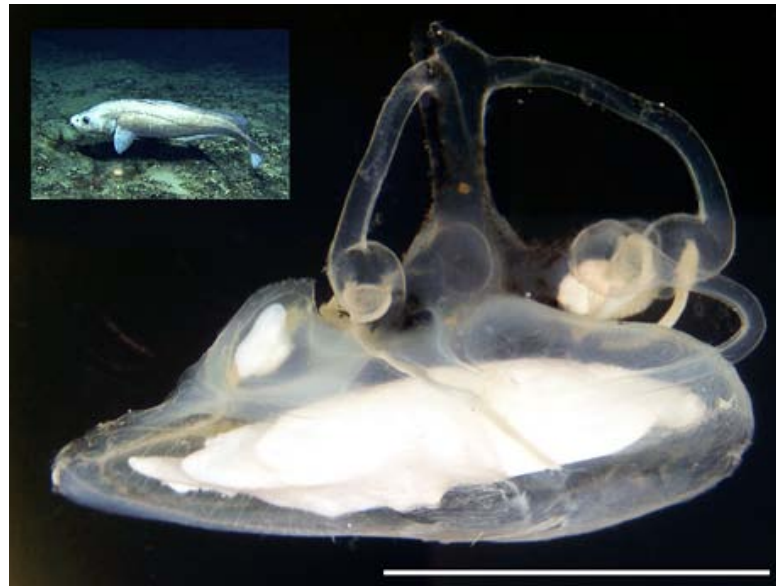


What are otoliths used for?

- Otoliths serve different functions although all functions are not well understood. It is thought that the lapillus is used mostly for gravity detection, as sensory hairs lining the sacs register movements of the otoliths.
- They discovered this by means of an experiment which replaced the otoliths with iron filings. When they placed a magnet over the fish it turned upside down.
- The saggita and astericus respond to inertia and sound stimulus.
- Collectively the otoliths provide sensory input needed for the fish to orient and balance itself in the water column and to detect sound (Caillet 1986).



"I think there's something wrong with my new Herring aid - it's giving me a Haddock."



Problems that occur with fish hearing vibrations underwater

- The density of a fish is almost the same as the density of the surrounding water, so it is hard for the fish to detect sound as it virtually moves through the body and doesn't reverberate for the sound detection to occur. Otoliths have a density three times that of the fish's body and this accounts for this problem.
- Sound moves slower when it travels through the air than through the water. This makes the direction of the sound very difficult to detect.

Sound has 2 pathways to the inner ear of a fish (Atema 1988):

- Direct – Sound moves directly to otoliths and is deflected off the otoliths, this vibrates causing shearing of ciliary bundles, almost small hairs, this triggers nerve transmission to the brain and sound is detected.
- Indirect – Found in most species with a swim bladder. Used more with species that have a close connection between swim bladder and inner ear, like carp and catfish. The sound enters the swim bladder and compresses the gas radiating sound energy in particle displacement causing the otoliths to vibrate and the fish can detect the sound. This is usually used for sound at frequencies above $\pm 200\text{Hz}$.



- Several studies have shown that fish can determine the range and direction of underwater sound at frequencies ranging from 0.1-1.0 kHz even in the presence of background noise.
 - Humans and other land animals directionalize sound using the time of arrival differences between our two ears.
 - Given that sound speed in water is about five times higher than that in air and the distances between the two ears in fish are no more than a few centimeters, fish must use a fundamentally different directionalization mechanism.
 - Most fish have two "inner" ears with no direct fluid connection to their environment. The fish ear consists of three endolymph-filled semicircular canals, each of which contains a bony mass, the otolith, suspended <100 microns above the macular membrane densely covered with more than 100,000 hair cells (similar to those found in our own ears). Incident sound oscillates the otolith, with its greater inertia, with respect to its surroundings (Figure 1).
 - Given that biological systems are optimal, why do fish need complex otolith geometries and so many hair cells?
- Current models of fish hearing assume that fish determine the direction of incident sound by detecting otolith motion along the direction of the acoustic wave--but these models fail to explain why fish need complex otolith geometries or so many hair cells.
 - The incident sound also creates a flow between the otolith and the macula.
 - Recent hypotheses suggest that the fish ear functions as an "*auditory retina*". In this hypothesis, the densely packed hair cells visualize the flow patterns due to the acoustically induced flow in the complex three-dimensional geometry between the otolith and the macula, much like a tuft visualization.
 - The complex geometry of fish otoliths may help to distinguish flow patterns for sound from different directions.
 - By converting acoustic signals into spatial patterns sampled with extremely high spatial resolution by the macular hair cells, directionalizing sound becomes a pattern recognition problem, not unlike the visual patterns imaged by the retina.

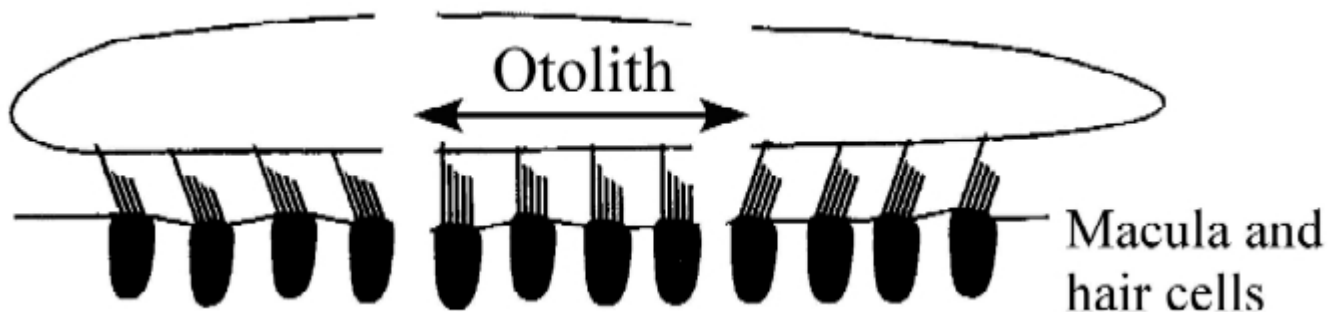


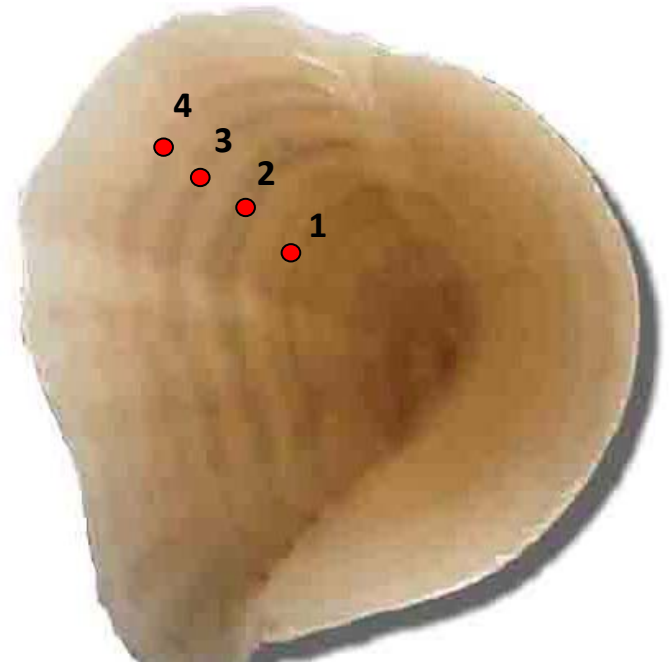
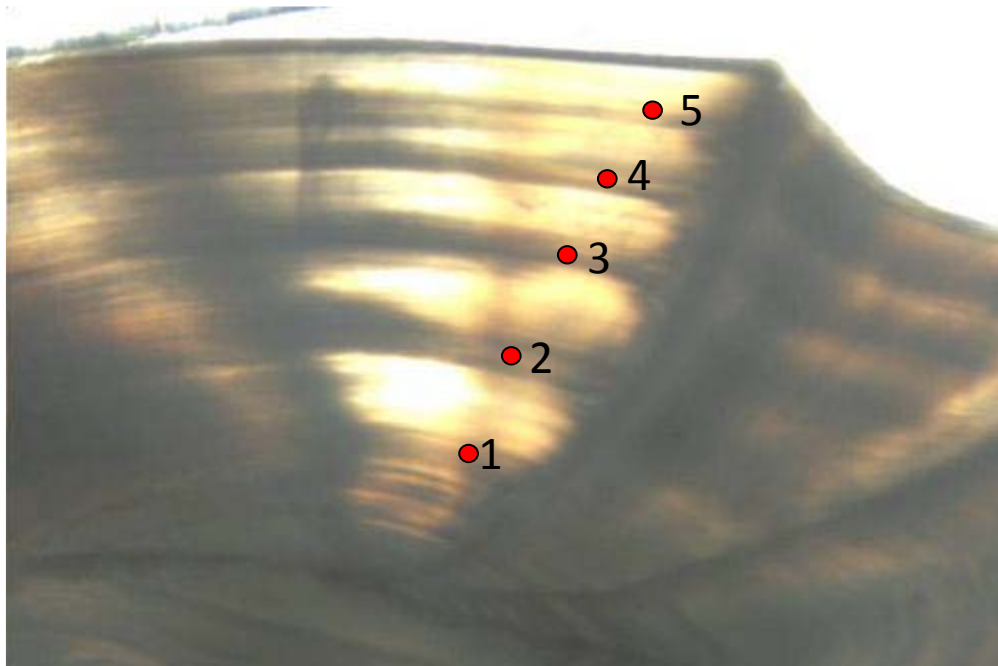
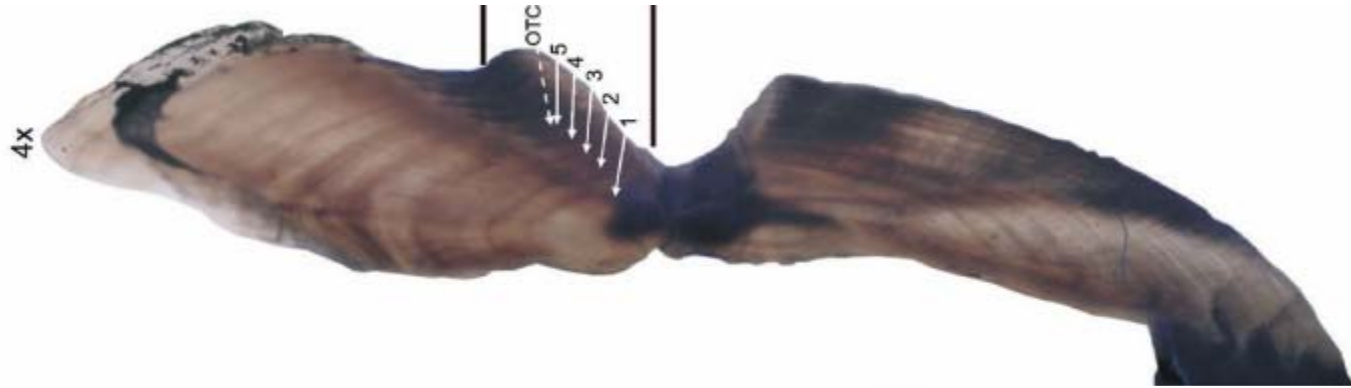
Figure 1 Otolith oscillating above the macular hair cells

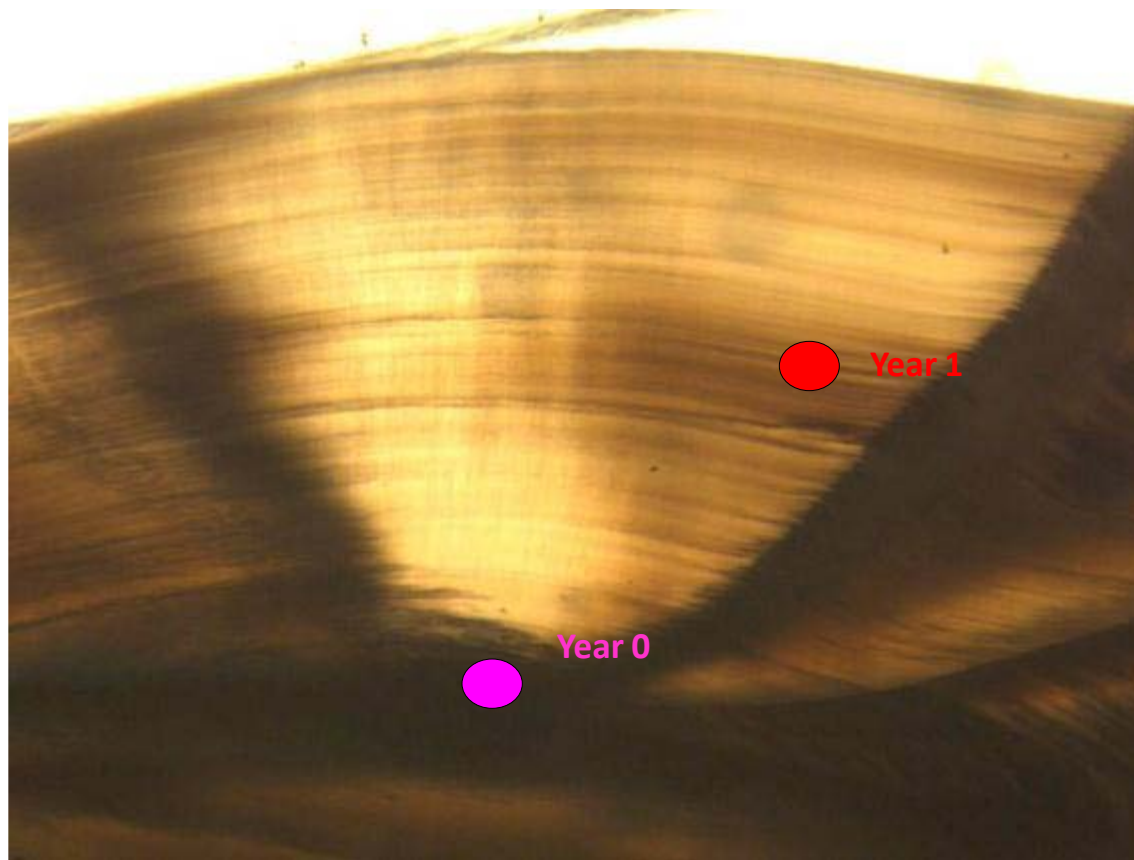
How do scientists use otoliths?

- Otoliths come in a variety of shapes and sizes and each otolith is unique to that species.
- As otoliths are enlarged at a rate similar to that of body growth, they show concentric rings (corresponding to slower and faster growth rates) which can be used to estimate the age of the fish.

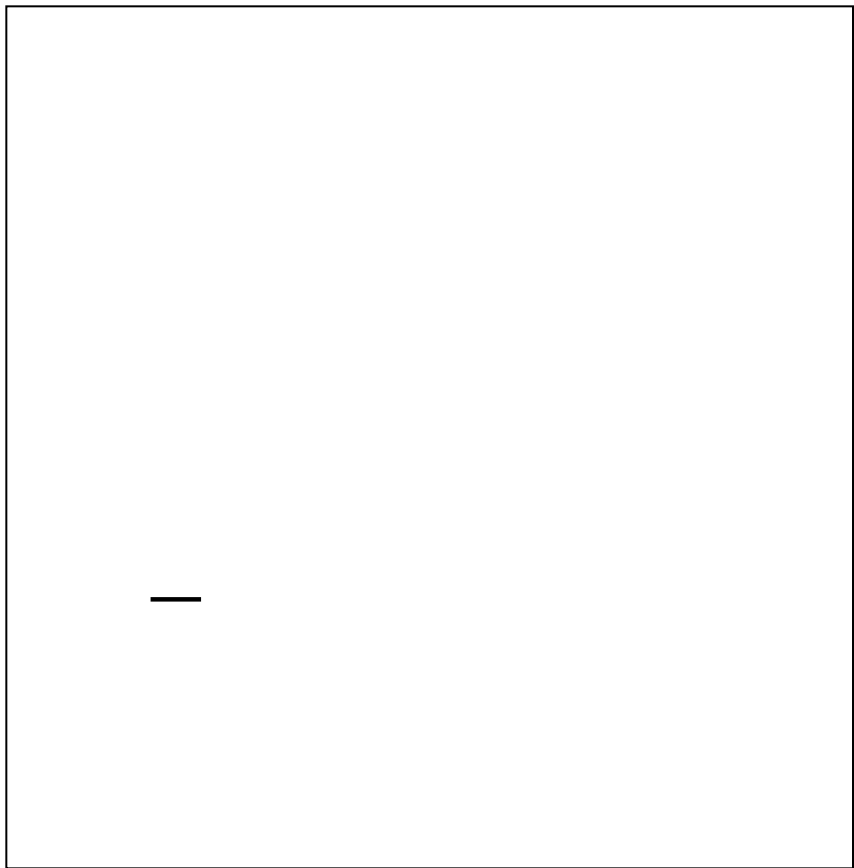


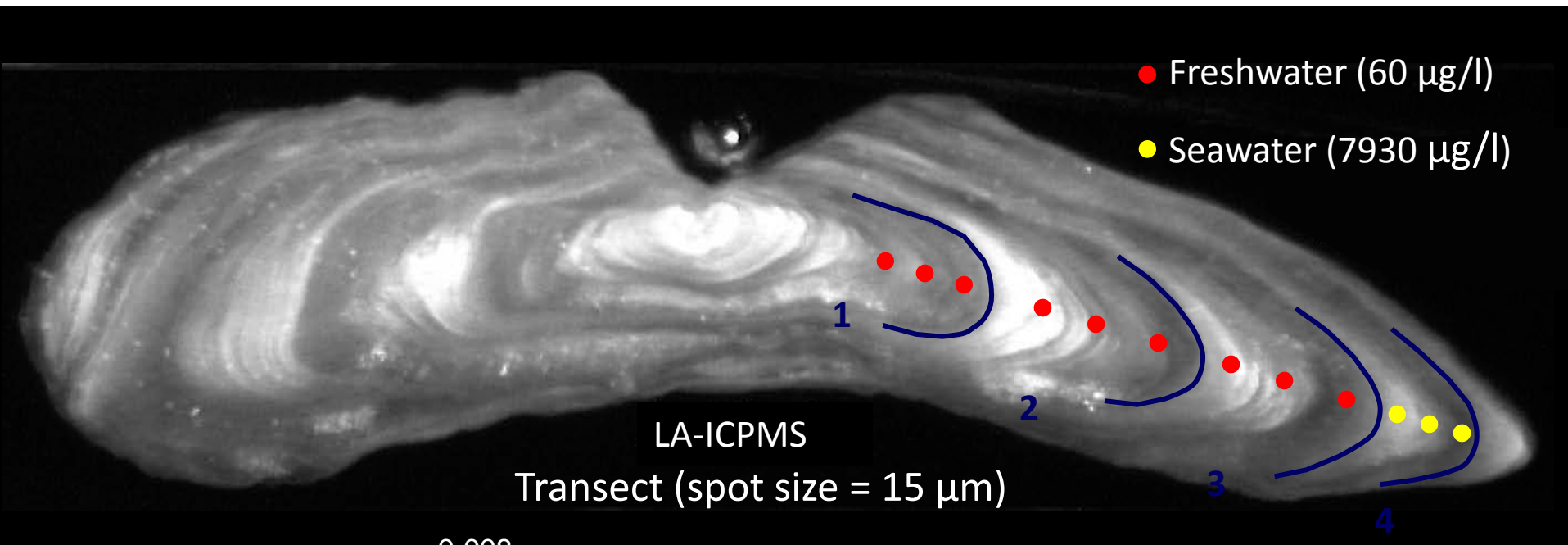
- The differences in summer (fast) and winter (slow) growth can be seen from a cross section of the otolith.



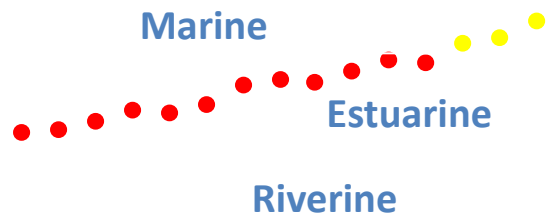


Year 0: Chemical signature natal estuary (Ba, Mg, Zn, Sr, Mn, Ca)





0.008



Otoliths can also be useful for scientists studying birds and mammals that eat fish as the otoliths remain indigested. The scientist can ID the fish prey by species by examining digested gut contents or fecal contents.

