SEM-II

Jaw Suspension in Vertebrates (G-S-A)

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3 vertebrates

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ert (1951), Walte... and (1982), Rome... and Miller (199... 2) have mentio... ebrae in their li... coelous, (b) proc... (d) heterocoelo... acoelous (Fig. ...

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Opisthocoelous vertebra

(Gk. opisthe = behind, Gk. coel = concavity)

When the centrum bears concavity at the posterior surface of the vertebra but the anterior surface shows convexity, a condition just reverse to the procoelous condition, is called **opisthocoelous** type vertebra. This type of vertebra is found in *Lepidosteus* (a primitive of bony fishes), some anurans (Discoglossidae, Pipidae, etc.), 2nd and 3rd cervicals of turtles, penguin and parrots. The cervical vertebrae of ungulates are, and the cervical vertebrae of dinosaurs were opisthocoelous.

In procoelous and opisthocoelous, the convex articular surface of one vertebra fits with the concave articular surface of another vertebra, thus acts a ball and socket joint permitting a greater flexion in all directions of the body.

Heterocoelous vertebra

(Gk. hetero = different, Gk. coel = concavity)

When the centrum of the anterior side of vertebra is convex dorsoventrally and concave from side to side, and the posterior face of the centrum is just reverse (concave dorsovenrally and convex from side to side), called **heterocoelous** vertebra, that is having a transverse, saddle-shaped surface in front and also saddle-shaped surface behind vertically (**Jollie, 1962**). Great freedom is the lateral and vertical flexion of the neck region but prevents in the rotation of the vertebral column, e.g., cervical vertebrae of birds.

Amphiplatyan vertebra or **Acoelous**

(Gk. amphi = both, Gk. platys = flat)

If the centrum of the vertebra is flat at both ends, it is called **amphiplatyan**, also known as **acoelous** (**Romer and Parsons, 1986**). This type of articular surfaces help to receive and distribute compressive forces within the vertebral column. These vertebrae are characteristic of mammals.

In some eels the anterior and posterior surfaces of the centra are flat (**Bond, 1996**). Infrequent types of vertebrae are seen in the vertebrates such as **biconvex type** (e.g., 9th vertebra of *Bufo* and *Rana*, 4th cervical of turtles), **platycoelous** meaning flat in front and concave behind, e.g., in some mammals, and **coeloplatyan** that is concave in front and flat behind, e.g., in some mammals (**Hyman, 1942**). **Jollie (1962)** mentions the term '**ginglymoidy**' in cases of double articular surfaces of the vertebra such as double convex, concave or asymmetrical.

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Phylogeny

Evolution of the vertebral column is not entirely clear, especially during its phylogenetic inception. The earliest vertebrates, such as fossils of *Myllokunmingia* and *Haikouichthys*, and the living hagfishes possess a notochord but lack vertebrae. In lampreys a few small cartilaginous elements are seen, but vertebrae are absent. In ostracoderms, we find a hint of vertebral column. Since then, the evolution of vertebral column in fishes and tetrapods is most complicated, because some parts of vertebral column are enlarged, others were lost, and some were evolved independently several times.

Skull

The skull or cephalic skeleton in vertebrates is a double structure—both embryologically as well as morphologically. During embryonic development two sets of bones of different origin join together in a unified way. The vertebrate skull is derived morphologically from two sources : the **neurocranium** (surrounding the anterior end of the nerve tube) and the **splanchnocranium** (encircling the anterior end of the digestive tube). The skull also plays double role—support and protection.

The skull starts its origin as paired cartilaginous plates (**parachordals**) situated one on either side of the notochord (Fig. 4.3A). Another pair of cartilaginous rods (**trabeculae**) develop in front of the parachordals. Simultaneously, cartilaginous investments start formation around three paired special sense organs—*olfactory capsules* around the organs of smell, *auditory capsules* around the ears and the *optic capsules* around the eyes. The olfactory capsules unite with the trabeculae, the auditory capsules unite with the parachordals and the optic capsules remain free. In

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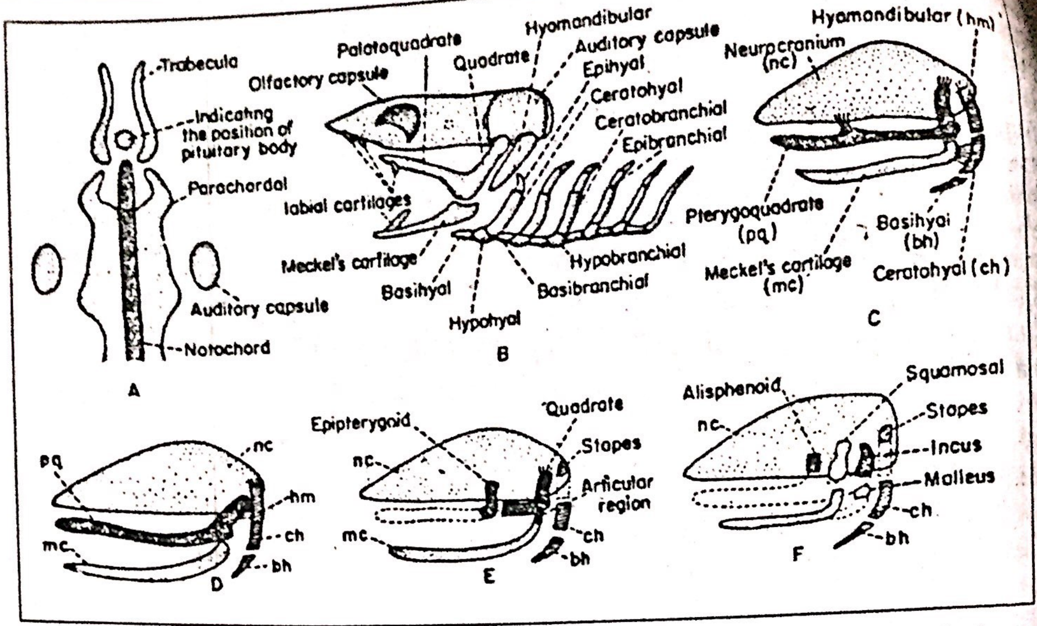

Fig. 4.3 : Development of skull. A. Embryonic cranial elements in Salmon. B. Side view of a cartilaginous skull showing the relationship with visceral arches. C–F. Showing different types of jaw suspension. C. Amphistylic condition. D. Hyostylic condition. E. Autostylic condition. F. Craniostylic condition.

course of development, the parachordals and trabeculae fuse into a single *basal plate.* This plate forms the floor of the skull and gives off vertical upgrowths on each side to give rise to the **brain-case** or **cranium.**

With the formation of cranial box different regions of the skull become distinguishable. The posterior or *occipital region* is developed from the parachordals and remains united with the anterior end of the vertebral column. It presents a large *foramen magnum* for the exit of the spinal cord. An *auditory region* is formed by paired auditory capsules. The other region, the *trabecular region* which includes : (i) an *interorbital region,* (ii) an *olfactory region* (two olfactory capsules with a median vertical septum mesethmoid) and (iii) a *rostrum* or *prenasal region* in front of the mesethmoid. The floor of the skull is called *basis cranii* which is developed from the basal plate. The roof is initially incomplete which becomes closed by membranes. The walls bear *foramina* or apertures for the exit of the cranial nerves. All these components are derived from the neurocranium.

Besides the neurocranial elements, there are other elements, called **visceral ba** (splanchnocranial elements) which particip in skull formation. Between the gill-slits the are series of cartilaginous rods like paired ha hoops around the pharynx. The visceral ba become united with one another to form th **visceral arches.** There are four to nine visce arches in vertebrates. Of the visceral arches, *first* or **mandibular arch** and the *second* or **hyo arch** participate in skull-formation while rest are known the **branchial arches** (Fig. 4.3

A list of derivatives of branchial arches sharks, teleosts and tetrapods is given in Tab 20.

In all vertebrates except the agnathans, mandibular arch becomes modified into ja The dorsal elements or the **palatoquadrates pterygoquadrate cartilages** become the up jaw while the ventral pair (*Meckel's cartila* form the lower jaw. The posterior end of **pterygoquadrate,** the *quadrate* provides articulation for the lower jaw. The hyoid also becomes divided into two parts—a do part, called *hyomandibula,* and a ventral p

Table 20 : A list of fates of the branchial arches in sharks, teleosts and tetrapods

Name of the Arch	Sharks	Teleosts	Amphibians	Reptiles and Birds	Mammals
1st or Mandibular arch	Palatoquadrate or Pterygoquadrate (upper part) Meckel's cartilage (lower part)	Quadrate Epipterygoid Articular	Quadrate Epipterygoid Articular	Quadrate Epipterygoid Articular	Quadrate Alisphenoid Malleus
2nd or Hyoid arch	Hyomandibula Ceratohyal Basihyal	Hyomandibula Ceratohyal Hypohyal Basihyal	Stapes (Columella) Ceratohyal Hypohyal	Stapes Ceratohyal Body of hyoid	Stapes Anterior horn of hyoid Body of hyoid
3rd or 1st branchial arch	Epibranchial Ceratobranchial Hypobranchial or 1st branchial arch	Epibranchial Ceratobranchial Hypobranchial or 1st branchial gill arch	Part of hyoid apparatus	Posterior horn of hyoid	Posterior horn of hyoid
4th or 2nd branchial arch	2nd branchial arch	—	Part of hyoid apparatus	Part of hyoid apparatus	Thyroid cartilages
5th or 3rd branchial arch	3rd branchial arch	3rd branchial arch	Laryngeal cartilages	Laryngeal cartilages	Laryngeal cartilages
6th or 4th branchial arch	4th branchial arch	Not found	Not found	Not found	Epiglottis (?)
7th or 5th branchial arch	5th branchial arch	—	—	—	—

— indicates absent.

designated as *hyoid cornu.* The hyoid cornu is divisible into *epihyal, ceratohyal* and *hypohyal.* The tongue is supported by a median *basihyal* which is attached with ceratohyal.

Jaw Suspension

The jaws are the characteristic feature of the gnathostomes which are used for holding the prey, and chewing the food materials. In the course of vertebrate evolution, the appearance of jaws has profoundly changed the mode of feeding. Before the appearance of jaws, the living animals like protochordates are the ciliary feeders. The cilia of the buccal funnel or in other parts of the body play a major role in food collection. In agnathans the mouth is suctorial. The ostracoderms collected their food, mainly algae or other organisms by scraping the rock surfaces.

Origin

The first visceral arch (**mandibular arch**) is modified into jaws and embrace it firmly to the chondrocranium. The upper part of the mandibular arch (epibranchial) becomes **palatoquadrate.** The lower part of mandibular arch (ceratobranchial) forms the lower jaw, also called **Meckel's cartilage.** The second visceral arch or **hyoid arch** is connected with the chondrocranium and acts as supporting structure. The upper part of second visceral arch is called **hyomandibula**. Next succeeding arches are called **branchial arches** and are connected to the respiration, not associated with the formation of jaws.

Definition

The mechanism by which the upper jaw (palatoquadrate) and lower jaw (Meckel's cartilage) are suspended from the neurocranium, is called jaw suspension.

Types of Jaw Suspension

Goodrich (1930, '58), **Walter** and **Sayles (1949)**, and **Weichert** and **Presch (1975)** have mentioned 4 types of jaw suspension. These are (i) Amphistylic (primitive elasmobranches), (ii) Hyostylic (Sharks and sturgeons), (iii) Autostylic (tetrapods other than mammals) and (iv) Craniostylic (mammals).

Hyman (1942) has mentioned 5 types of jaw suspension. They are as (i) Amphistylic (primitive sharks), (ii) Hyostylic (most elasmobranchs), (iii) Autostylic (most vertebrates), (iv) Holostylic (holocephali), and (v) Methylostylic (teleostomes). **Young (1981)** has also mentioned 5 types but in different names in some groups. **Kardong (2002)** refers to 6 types of which **palaeostylic** is referred to agnathans where none of the arches attach themselves directly to the skull.

The splanchnocranium is attached with the neurocranium to form a full-fledged skull. Five principal types of such attachment are encountered in vertebrates (Fig. 4.3C–F). They are : **Autodiaslylic, Amphistylic, Hyostylic, Autostylic** and **Craniostylic**. In the first three types of jaw suspension the pterygoquadrate, the hyomandibular or both are involved while in the fourth variety attachment is done by investing bones.

Autodiastylic

It is a form of jaw suspension in which the upper jaw (palatoquadrate) is suspended from two articulations with the cranium. The suspended structures are ligaments which hang both at its front as well as hind end of the cranium. The hyoid arch remains an almost typical branchial arch, neither modified, nor to support the jaw. This is the most primitive type of jaw suspension, found in acanthodians.

In some sharks such as *Chlamydoselachus* (frilled shark), *Hexanchus* (six-gilled shark), *Notorhynchus* (broad nose seven gill shark), the squaloids (dog fish shark), pristiophoroids (saw sharks) and *squatina* (angle shark) the orbital process is on the palatoquadrate and an attachment to the orbit is seen. This type of a few suspension is referred to as **Orbitostylic** by **Maisey (1980)**.

Amphistylic condition (both pillar)

This type of jaw suspension is found in a few primitive elasmobranchs (like *Heptranchias*). In this type of jaw suspension both the pterygoquadrate and hyomandibular make direct articulation with the neurocranium (Fig. 4.3C). The pterygoquadrate articulates at two points : (i) a *basal process* and (ii) an *otic process*. The hyomandibular also articulates with the auditory capsule.

Hyostylic condition (hyoid pillar)

This type of jaw suspension is found in most modern elasmobranchs and all bony fishes. In this type of jaw suspension the hyomandibular alone acts as the suspensorium of the jaw (Fig. 4.3D). In bony fishes (like *Amia, Lepisosteus* and others) the typical hyostylic condition is modified where a *quadrate* develops from the posterior portion of the pterygoquadrate which articulates with an *articular* bone. The articular is developed from the Meckel's cartilage.

Remark

Hyman (1942) refers to the **methylostylic type** of jaw suspension in case of teleostomes in which palatoquadrate is suspended mainly from the otic capsule by way of hyoid derivatives.

Autostylic condition (self pillar)

This type of jaw suspension is found in dipnoans, amphibians, reptiles and birds where the upper jaw is articulated immovably with the neurocranium without the interven-

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tion of the hyomandibular. The articulation is done by the quadrate of the upper jaw and the articular of the lower jaw (Fig. 4.3E). In holocephalians and lungfishes the typical autostylic condition is modified where the entire upper jaw becomes completely fused with the neurocranium.

Autostylic is divided into the following subtype

Holostylic

In Holocephali (Chimaeras) the upper jaw (palatoquadrate) is firmly fused to the neurocranium (brain-case) and lower jaw is suspended from it. Hyoid arch becomes complete and remains free behind.

In some lizards, snakes and birds the quadrate is loosely attached.

Craniostylic condition

This type of jaw attachment is found in mammals. This is a modified type of autostylic condition. As the articular and quadrate become transformed into *malleus* and *incus* (ear ossicles) respectively, the articulation of the jaw is done by two pairs of investing bones—the *squamosals* of the upper jaw and the *dentaries* of the lower jaw (Fig. 4.3F).

Remark

Hyman (1942) refers to that the jaw suspension of mammals is undoubtedly derived from the autostylic type.

ORIGIN OF VERTEBRATES

Since the inception of evolutionary concept that living organisms transmutated through the ages, the question of searching the ancestry of vertebrates has become a central problem in Biology. Extensive work has been done on this particular problem. The greatest difficulty confronting the workers on this line is the lack of good fossil records of their earlier representatives. Many nonchordates have been brought to the forefront in unravelling the vertebrate evolution. It will not be an exaggeration to point out that almost all the nonchordate phyla have been suggested that hold the key of vertebrate evolution. But many workers do not accept the idea of derivation of vertebrates directly from any specialised adult nonchordate. The dynamic larval stage of some nonchordate forms are claimed to be the possible progenitor of early chordates which have evolved further to give rise to higher forms.

A good many views are extant on the origin of vertebrates. Some of the views are old and they have been mentioned as pieces of historical importance. Since long time it was regarded that the invertebrate chordates, originating from some nonchordate source, have given the origin of the vertebrates. The logical evolutionary trend is as follows :

Nonchordates → invertebrate chordates → vertebrates

But this concept is not accepted by recent workers in this line (*vide* **Barrington, 1965**) which is discussed in the last portion of this chapter.

BIOLOGICAL ORGANISATION

The chordates constitute a very large group which includes the invertebrate chordates and vertebrates. They possess some identifying features. These features are again repeated to draw parallelism between the vertebrates and the nonchordates in the phylogenetic discussion of the vertebrates. These features are :

1. Body is bilaterally symmetrical.
2. A dorsal tubular nerve cord is present. The anterior part becomes specialised into a brain in the vertebrates.
3. Notochord is present at least in some stage of life-history.
4. The pharynx is perforated by gill-slits.
5. The coelom is enterocoelous in origin.
6. Cephalisation is well-marked.
7. Metamerism is present.
8. A pulsating organ or heart is present in the ventral side of the body.

SD Sir

Cranial kinasis =>

Kinasis -> It is defined as the movement within the skull and movement b/w the upper jaw and the brain case about the respective joints b/w them.

eg - anci fishes, bony fishes, early amphibians, most reptiles, birds and rephial ancestors to mammals

It is not present in modern amphibian, turtles crocodiles and mammals.

Akinatic skull : No such movement b/w the upper jaw and brain case is found here. Loss of kinasis in mammalian skull allows infants to suckle easily. Juveniles and adults can chew firmly with sets of specialize teeth that work accurately.

Jaw-suspension variation :

A] Fish ->

Plackoderm => Jaws are powerful and self-bracing with chondocranium by ligments and the hyo mandibular was free.

Dipnoan => The hyomandibular takes no share in the support of the jaw. and may become much reduced.

e.g - Lepidosiren, protoctерous

The 3 sides of articulation occured b/w the upper jaw and chondrocranium is —

i) anterior palatine process with anterior orbital.

ii) middle basal process with trabicula

iii) Posterior otic process with auditory capsule.

Holocephali => characterized by the presence of a specialized autostylic suspension. Upper jaw fused to cranium.

both in the ethmodial region infront of the eye and in the region of ear. Hyomandible is free. both from upper jaw and cranium.

Crossopterygii => In the coelacanth the jaw is autostylic in nature and the upper jaw is attached to the anterior division of the skull.

Jaw suspension :

11/03/15
(SD sir)

Can be defined as the opposable articulated structure, at the entrance of mouth, typically derived from be most anterior to pharyngeal arches and used for grasping and manupulating food.

Functional advantages :-

i) Functionally autostylic condition provided stability to strengthened the bite of the jaw, during crushing of solid food in placoderms.

ii) In Dipnoan, autostylism was developed independently in order to provide maximum stability during feeding.

iii) In crossopterygian, autostylism leads to the movement of the upper jaws on their articulation to the cranium. This movement was to enlarge the gaps of the mouth and to protect the brain from shock when the jaws were functioning.

B] Amphibians :

Modern amphibians have autostylic jaw suspension where the quadrate of the upper jaw articulates with squamosal without an assist from the hyomandibular.

The freed hyomandibular cosequently evolved as collumella or stepis - the first of the ear ossicles to have evolved. Of the 3 attachment points b/w upper jaw and chondrocranium the basal process which is present in Urodela but not in A articulates with trabecula. Besides the palatine process which generally articulates with anterior orbital is little developed in many urodella.

Functional advantages :-

i) This type of jaw suspension improve the efficyency of muscles for opening the jaws and gain on it leverage in articulation.

C] Reptile

In most reptiles the quadrates and articular bone serve as the sight of articulation of the jaw. In chelonia and crocodilia the quadrate is firmly fixed to the auditory region of skull consisting a diff.

But in lizard and snakes the skull is st where the quadrate is supported away from the skull and is free to move. In synapsic reptiles the lower jaw articulates directly to the skull free in articular and quadrate which transform into Malius and Incus respectively into the middle ear.

developed for sound conduction. Consequently the articulation in b/w 2 dermal bones — squamosal of upper jaw and the den of lower jaw. This new articulation is named as craniostylic jaw suspension.

Functional advantages:-

The significant development of craniostylic jaw suspension was due to development of characteristic grinding teeth (heterodont condition) in upper and lower jaw. The rigidity required by such feeding mechanism is provided by craniostyli. The autostylism in higher forms of vartibrates has been specially developed for the enhancement of hearing mechanism.

Amphistylic condition :

This type of jaw suspension is found in few primitive elasmobranch like Heptranchias. Here, both the pteregoquadrate and hyomandibular make the direct articulation with neurocranium. The pteregoquadrate articulates at 2 points : a basal process and an otic process. The hyomandibular articulates with auditory capsules

Hyostylic condition :

Found in most modern elasmobranch and all bony fishes. The hyomandibular alone acts as the suspensorium of the jaw. In bony fishes the typical hyostylic condi. is modified where a quadrate develops from the post. part of pteregoquadrate which articulates with an articular bone. The articular is developed from the Meckel's cartilage.

Functional advantge :-

1) Amphistylic jaw suspension provides maximum stability and rigidity of jaws for feeding on hard food and is thus adaptive to be active predacious habit of the individuals. by increasing the power of bite.

In hyostylic condition, it provides maximum mobility required for changed feeding habit of higher fishes. and helps in functioning of mouth as an efficient grasping and suctorial organ.

Hyostyli leads to a protrusable job in modern sharks helps in plucking of benthic food stuff.

Autodiastyli condition :

It is a form of jaw suspension in which the upper jaw is suspended from 2 articulations with the cranium. The Hyoid arch remains an almost typical branchial arch neither modified nor to support the jaw. This is the most primitive type of jaw suspension find in Acanthodians.

~~Sweat sebaceous mammary~~

~~hair (ultra structure)~~

~~Stages of formation of mammalian horn antler.~~

18/03/15

[SD Sir]

Craniostylic

Autostylic → Amphistylic → Osteichthyes

Hyostylic

Evolution of jaw and jaw suspension :

Evolution of the jaw is open traced through how the mandible is attached to the skull. Agnathan represents the early paliostylic stage in which none of the arches attach themselves directly to the skull. The earliest jaw condition euautostylic found in plackoderms and primitive fishes where the mandibular arch is suspended from the skull by itself without help from the hyoid arch. In early sharks, some osteichthyes and crosopteregians jaw suspension is amphistylic that is the jaws are attached to the brain case through 2 articulation, anteriorly by filament connecting Palatoquadrate to the skull and posteriorly by hyomandibula. Many perhaps most modern sharks exibit a variation of amphistylic jaw suspension. In most modern bony fishes jaw suspension is hyostylic because the mandibular arch is attached to brain case permanantly through hyomandibulum and thus opening a new dermal element, symplectic bone. The viseral cranium remains cartilagenous in elasmobranch but in bony fishes and tetrapodes ossification center appears, forming distinct bony contributions to the skull.

In most amphibians, reptiles and birds jaw suspension is metaautostylic – jaws attached to brain case directly through quadrate (Post. part of palatoquadrate). The hyomondibulum plays no part in supporting the jaws. It give rise to slender columella or stepis. Other eliments of the 2nd and 3rd visceral arch contribute to the hyoid apperatus – that support tounge and floor of mouth.

In mammals, jaw suspension is cranio-stylic.
The entire upper jaw is incorporated in brain case but lower jaw is suspended from sqamosal bone of brain case. The lower jaw of mammals consist of dentary bone. The palatoquadrate and Meckel's cartilage sill remain cartilageneous except at post. end and gives rise to Incus and Malius – as the middle ear ossicle respectively. Thus in mammals splanchocranium does not contribute to the adult jaw but forms styloid and 3 middle ear-ossicles.

In man, 4th and 5th visceral arch from the laryngeal cartilages which helps in sound production. 6th visceral arch modified into epiglotis and 7th one forms tracheal rings.

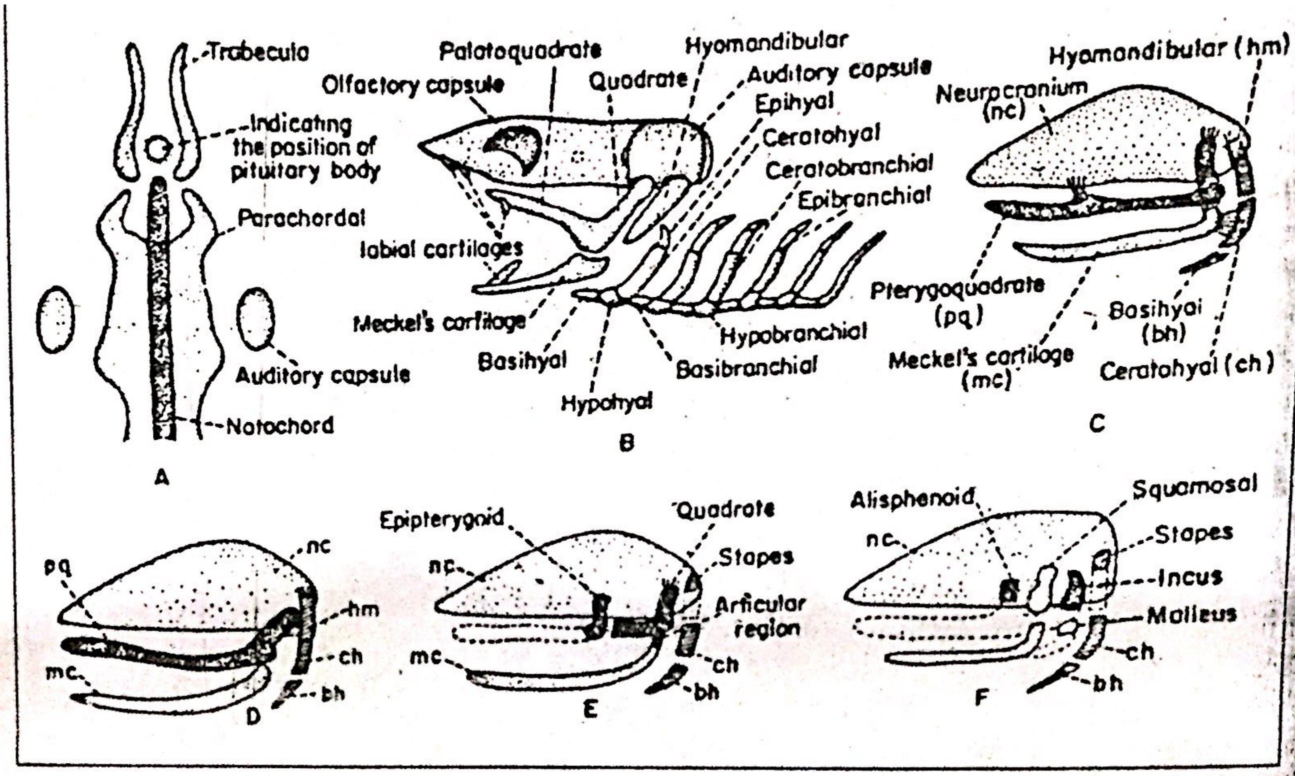

Fig. 4.3 : Development of skull. A. Embryonic cranial elements in Salmon. B. Side view of a cartilaginous skull showing the relationship with visceral arches. C–F. Showing different types of jaw suspension. C. Amphistylic condition. D. Hyostylic condition. E. Autostylic condition. F. Craniostylic condition.

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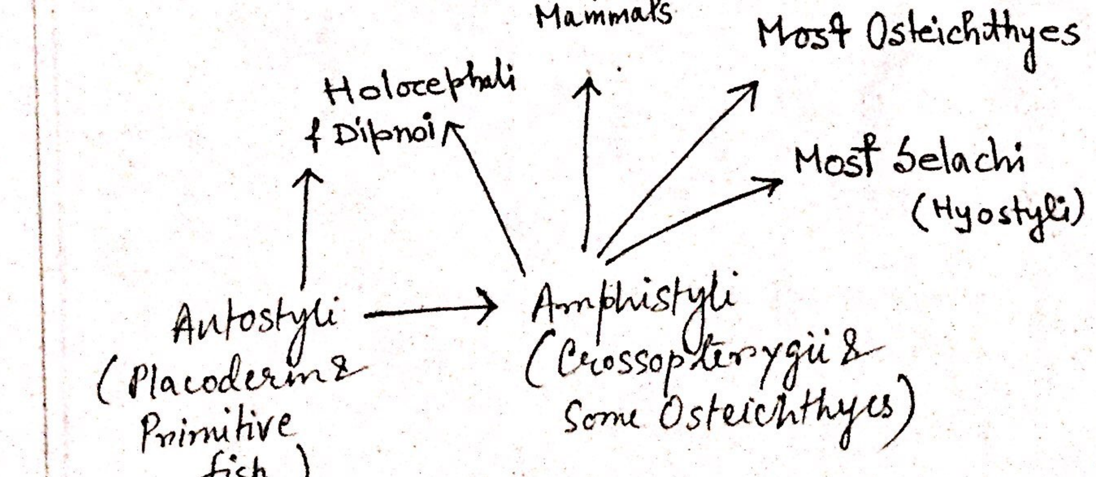
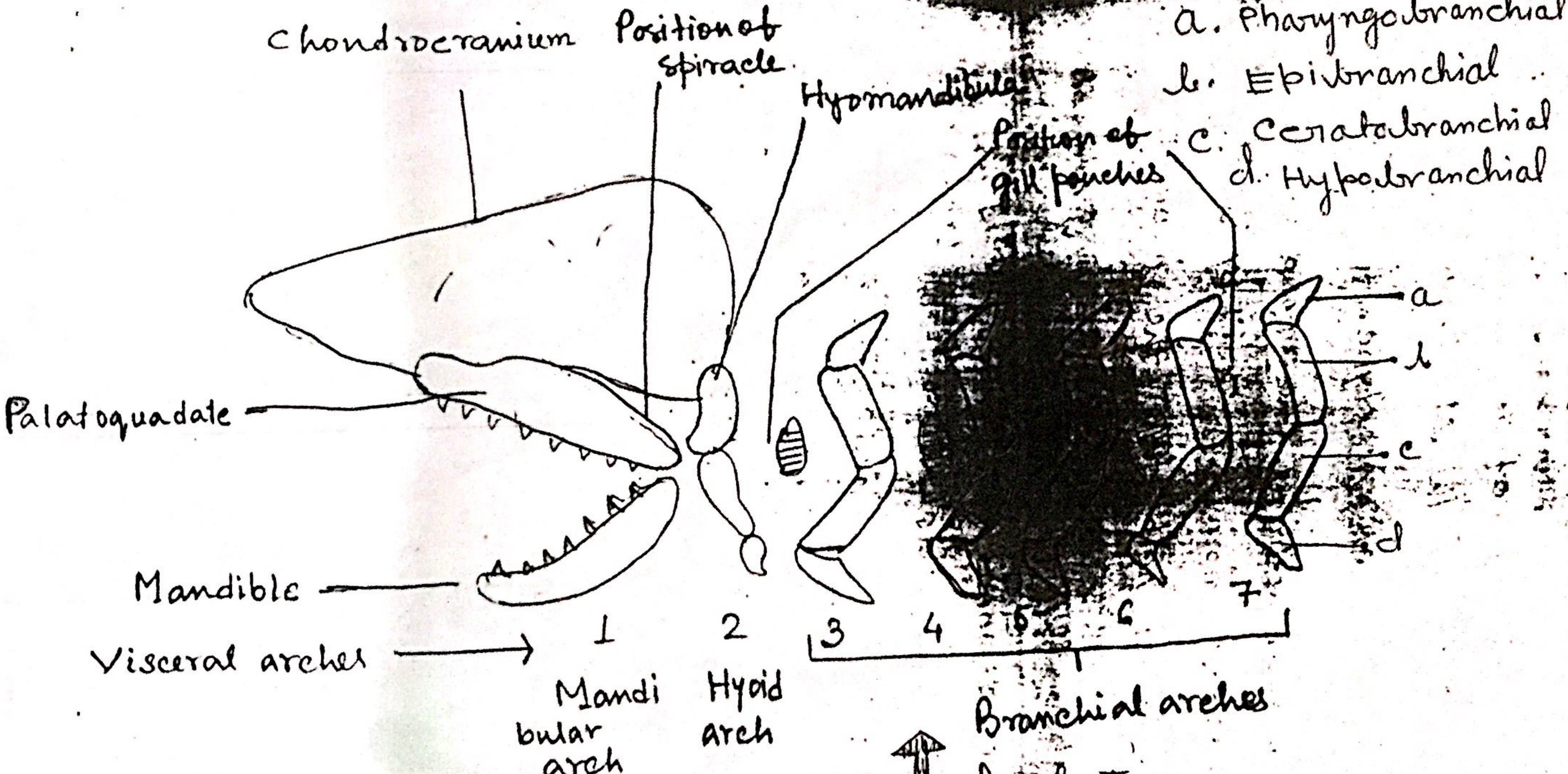
With the formation of cranial box different

Besides the neurocranial elements, th are other elements, called **visceral b** (splanchnocranial elements) which particip in skull formation. Between the gill-slits th are series of cartilaginous rods like paired h hoops around the pharynx. The visceral b become united with one another to form

Phylogeny of Jaw Suspension





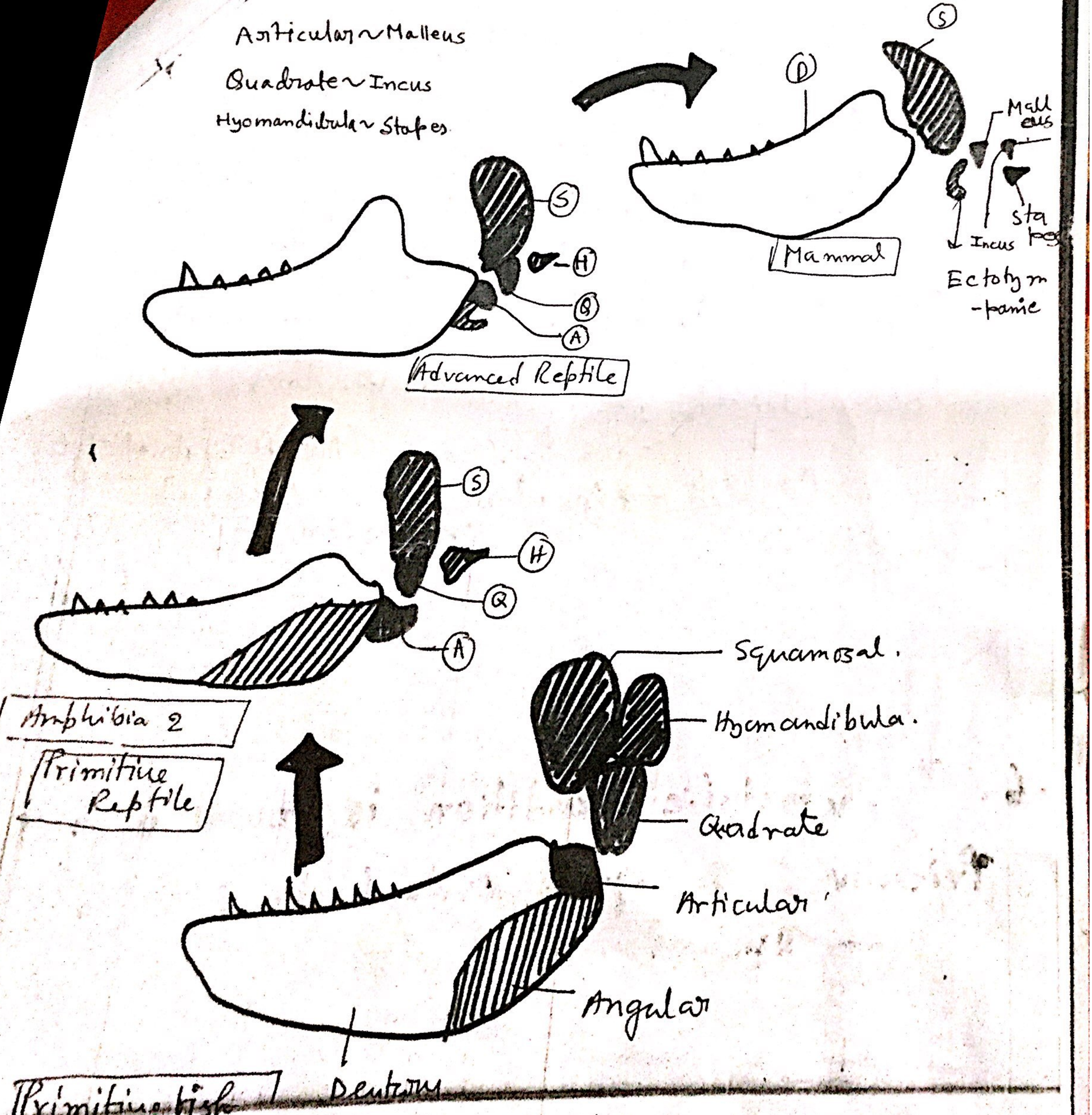
B. Development of Jaw

A. Jawless

Debarati Mukherjee

I

Articular ~ Malleus
Quadrate ~ Incus
Hyomandibular ~ Stapes



" Evolution of Jaw bones in Vertebrates"

Jawless chordate
↓
100 visceral arch (branchial arch)
↓
Perform respiration & filter feeding
↓
Taking micro organism from current of water
↓
Microphagus food habitat
↓
Evolution of Jaw
↓
Particulate feeding habitat
↓
Active participation of Hyomandibula
↓
Change of Jaw Suspension; changed Cranial kinesis
↓
Changed feeding (Autostyli, Amphistyli, Hyostyli)

In Man → Craniostyli → Ear ossicle → Sound Conduction

In Man:
- I → Jaw
- II + III → Hyoid → for hard food crushing
- IV + V → Laryngeal cartilage → Sound production
- VI → Epiglottis
- VII → Trachea → Respiration