Lesson 15

◊ **Lesson Outline:**

- The Skull
  - Neurocranium, Form and Function
  - Dermatocranium, Form and Function
  - Splanchnocranium, Form and Function
    - Evolution and Design of Jaws
    - Fate of the Splanchnocranium
- Trends

◊ **Objectives:**

At the end of this lesson, you should be able to:

- Describe the structure and function of the neurocranium
- Describe the structure and function of the dermatocranium
- Describe the origin of the splanchnocranium and discuss the various structures that have evolved from it.
- Describe the structure and function of the various structures that have been derived from the splanchnocranium
- Discuss various types of jaw suspension and the significance of the differences in each type

◊ **References:**

- Chapter: 9: 162-198

◊ **Reading for Next Lesson:**

- Chapter: 9: 162-198

The Skull:

From an anatomical perspective, the skull is composed of three parts based on the origins of the various components that make up the final product. These are the:

Neurocranium (Chondocranium)
Dermatocranium
Splanchnocranium

Each part is distinguished by its ontogenetic and phylogenetic origins although all three work together to produce the skull.

The first two are considered part of the Cranial Skeleton.

The latter is considered as a separate Visceral Skeleton in our textbook. Many other morphologists include the visceral skeleton as part of the cranial skeleton. This is a complex group of elements that are derived from the ancestral skeleton of the branchial arches and that ultimately gives rise to the jaws and the skeleton of the gill arches in fish as well as to a series of derived structures in fish and tetrapods.

1) Neurocranium (Chondocranium)

a) Form

The neurocranium is the part of the skull that

- protects the brain and certain sense organs
- arises as cartilage (in all vertebrates)
- is subsequently replaced partly or wholly by bone except in cartilagenous fishes (Agnatha and Chondrichthyes)

Cartilagenous stage

Parachordal and prechordal cartilages and notochord

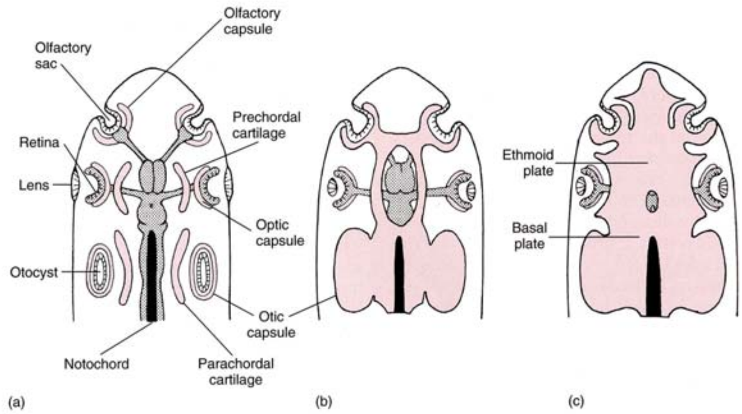
Condensation of cells derived primarily from neural crest cells and mesenchyme of mesodermal origin (sclerotome) form elongate cartilages underneath the brain (prechordal and parachordal cartilages), as well as supporting cartilages for the sensory capsules associated with the nose, eyes and ears.

The pre and parachordal cartilages expand until they meet in the midline forming plates under the brain that grow and fuse together to form the ethmoid and basal plates.

Sense capsules

The nasal, and otic cartilages become the nasal, and otic capsules. These subsequently fuse with the neurocranium.

The optic cartilage forms a capsule around the retina and develops, not into the eye socket, but into the sclerotic coat that becomes the fibrous wall of the eyeball in mammals. It does not fuse with the rest of the neurocranium.



Completion of the floor, walls and roof

The basal and ethmoid plates unite with the olfactory and otic capsules to form the floor of the braincase. The occipital cartilages from the developing spinal column grow upward and around the nerve cord to form the occipital arch. These form the posterior wall of the brain case and produce the opening, the foramen magnum, through which the spinal cord emerges. In some craniates there is the further development of cartilagenous walls around the brain and a cartilagenous roof. This is believed to be an ancestral condition.

Cartilagenous neurocrania of adult craniates

In agnathans and elasmobranchs, the chondrocranium does not ossify. The cartilage grows further upward and over the brain to complete the protective walls and roof of the braincase. (In most other vertebrates, the neurocranium forms a supporting floor for the brain but does not encase it). There are some species of fish (chondrosteans and dipnoans) that also retain a cartilagenous neurocranium throughout life.

Neural Ossification Centres

In most other vertebrates, the chondocranium becomes partly or completely ossified forming the endoskeleton portion of the brain case. (Your text goes into this process in detail but we will not).

These endoskeletal elements, along with the brain and sensory organs they support become enclosed in exoskeletal bone, derived from the dermis (We will discuss this next).

b) Function

The function of the neurocranium is:

- protect the brain and sensory structures
- provide attachment sites for jaw muscles

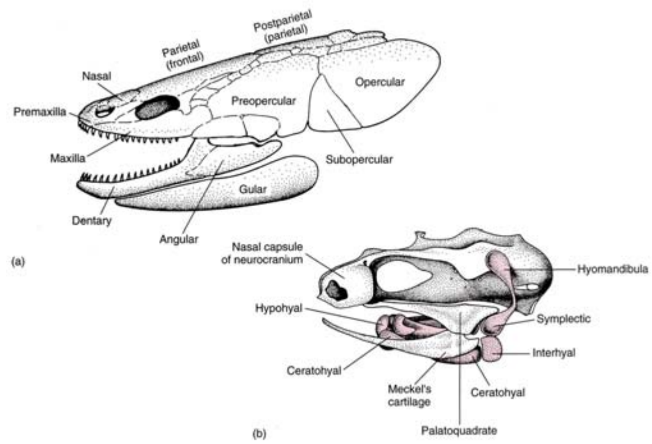
This, in part determines the form of the neurocranium.

2) Dermatocranium

The Dermatocranium forms from dermal bones and in later vertebrates forms most of the skull. It forms from intramembranous bone (no cartilage intermediate).

Evolution
The bodies of the earliest vertebrates were encased in dermal armour, itegumentary scales. It is believed that bony plates within the dermis (which stretches tightly over the skull) became an integral part of the skull. The neurocranium is endoskeletal, the dermatocranium is exoskeletal.

a) Form:
Basic Structure
The dermatocranium can be divided into:
Roofing bones that form above and alongside the brain and neurocranium.
Dermal bones of the upper Jaw.
Dermal bones of the primary palate.
Opercular bones.



b) Function:
Provides a protective shield over the brain and special sense organs.
Overlays or ensheaths the visceral skeleton forming the upper jaw and is tooth bearing.
Covers and protects the underside of the neurocranium.
Covers and protects the gills in bony fishes.

Again, note: the dermatocranium forms from dermal bones and in later vertebrates forms most of the skull; the neurocranium forms a bottom platform on which the brain rests and the brain and neurocranium become encased in exoskeletal bone.

3) Splanchnocranium

The splanchnocranium (or visceral skeleton) is the name given to the gill arches and their derivatives. These include the jaws.

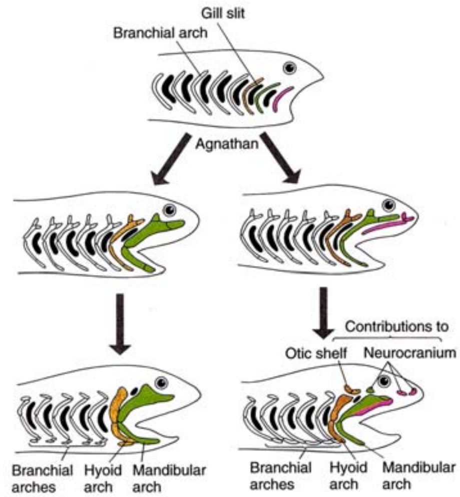
Evolution
The splanchnoderm is an ancient chordate characteristic. Its forerunner was associated with supporting the filter feeding structures of cephalochordates and urochordates.

Gill Arches III-VII

a) Form:

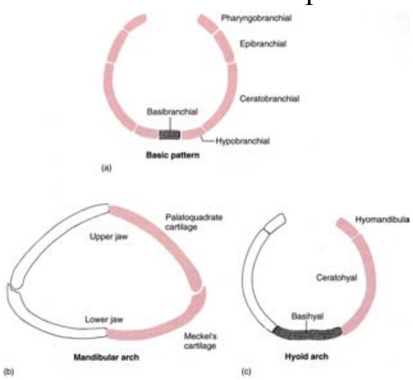
Among the fishes, the splanchnocranium derived from arches III-VII supports the gills and offers a site for attachment of the respiratory muscles.

Embryologically they are derived from neural crest cells. These cells move down from the sides of the neural tube and move into the walls of the pharynx between successive pharyngeal slits and differentiate to become the pharyngeal arches. Because of their association with the respiratory gill system they are also referred to as branchial arches or gill arches.



(a) Serial theory (b) Composite theory

Each arch can be composed of ***up to*** five articulated elements per side. Beginning dorsally these are:



- pharyngobranchial
- epibranchial
- ceratobranchial
- hypobranchial
- basibranchial

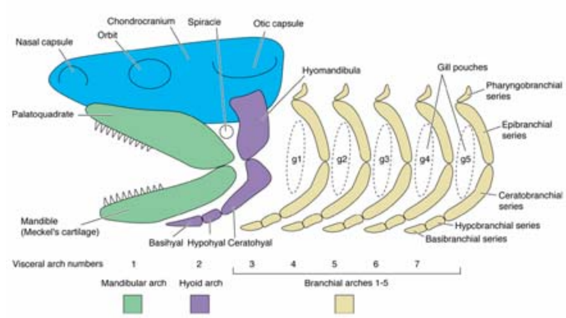


Fig. 7.3

The anterior two pair of arches move forward to border the mouth and become jaws. In most fish, five arches remain to support the gills.

b) Function:

While the branchial arches still play some role in feeding in those species of elasmobranchs that have secondarily returned to a filter or suspension-feeding mode, in most, the arches support the gills and have become a respiratory structure. The arches, however, not only serve to support the gills but also serve as sites for attachment of some respiratory muscles. (Note these are not the main muscles of the respiratory pump but muscles involved with controlling the position of the gills and the opening of the gill slits.)

Gill Arches I-II

a) Form: Evolution and Design of Jaws

The first fully functional arch of the jaw is the mandibular arch. This is the largest of the modified branchial arches. It is composed of the palatoquadrate cartilage dorsally and Meckel's cartilage ventrally.

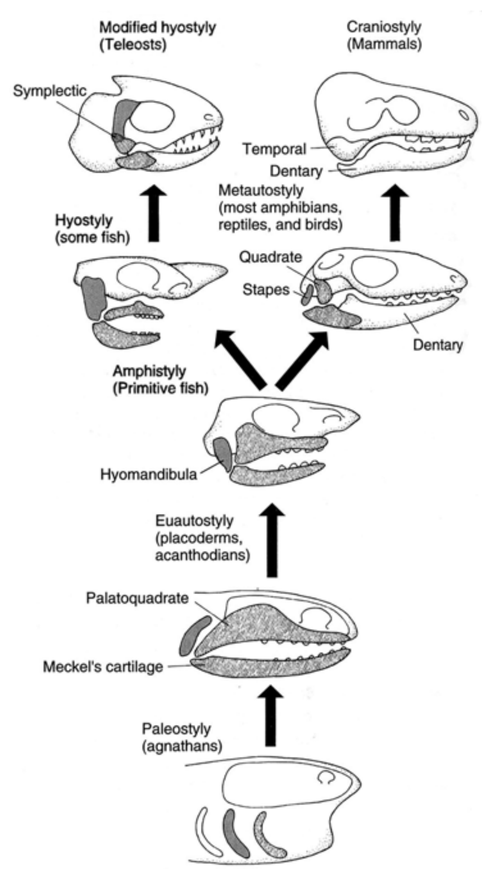
The second arch is the hyoid arch composed of the hyomandibula, ceratohyal, and basihyal cartilages.

In Chondrichthyes, a reduced gill opening, the spiracle, remains between the hyoid and mandibular arches. The origin of the elements from neural crest cells, the pattern of distribution of nerves and blood vessels and the origin of muscles all suggest that the jaws are derived from branchial arches.

While there is debate over the precise origin of the mandibular and hyoid arches from embryologic and ancestral arches, it is now routine to refer to the mandibular arch as the first branchial arch, the hyoid as the second branchial arch and the subsequent five arches as branchial arches III to VII. (See Table 9.4 in your text).

b) Function: Jaw Suspension

The earliest type of attachment is referred to as ***Paleostyly,*** which is a bit of a misnomer since these animal lack jaws and there is no attachment. This is the situation currently found in the Agnathans. In this condition, neither the mandibular nor the hyomandibular arch is attached to the skull. There are no jaws.



The earliest type of jaw was one where the mandibular arch was attached by the palatoquadrate to the skull alone with no support from the hyomandibular arch. There are no living vertebrates today that exhibit this style of attachment but it was found in the placoderms and acanthodians.

In ancient sharks, the hyomandibula and one or more processes of the palatoquadrate were braced independently against the braincase. This is referred to as amphistylic

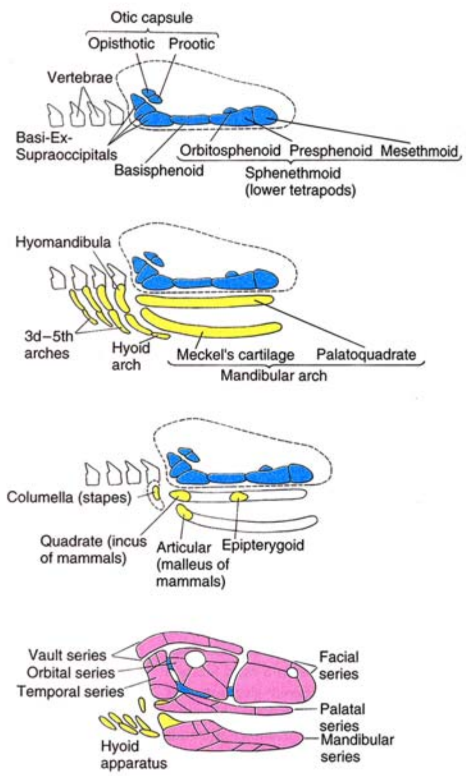
In the modern sharks and some of the earliest fishes, the jaw was attached to the braincase at the front by a ligament and at the back by the hyomandibula. Your book refers to this as ***Hyostylic***. With this advance, the hyomandibula now braces and supports the jaw but the entire complex is loose and quite dynamic.

In most bony fishes the jaw suspension is now a modified version of ***Hyostylic***. With this form of suspension, the main attachment of the jaw to the skull is by the hyoid arch.

In most amphibians, reptiles, and birds, the jaw suspension is ***Metautostylic***. The jaw is attached to the braincase through the quadrate – a bone formed from the posterior part of the palatoquadrate. The hyomandibula no longer contributes to the jaw but becomes the stapes.

In mammals, the jaw suspension is ***Craniostylic***. The entire upper jaw is incorporated into the braincase. The lower jaw is suspended from the temporal bone, a dermal bone from the braincase. The lower jaw is composed of a single dermal bone, the dentary bone. The palatoquadrate and Meckel's cartilage remain cartilagenous except at their posterior ends, which give rise to the incus and malleus of the middle ear (ie: the splanchnocranium no longer contributes to the jaw or its suspension).

Fate of the Splanchnocranium



Note: overall there is a progressive reduction in the contribution from splanchnocranium and replacement with dermal bone

- Meckel's cartilage becomes encased in dermal bone (the dentary), which now forms the lower jaw. The posterior end protrudes as the articular bone, which articulates with the upper jaw.
- the maxilla and premaxilla form the upper jaw. In most vertebrates, all that remains of the splanchnocranium is the quadrate bone, which continues to serve as the articulation with the lower jaw.
- this trend occurs in both tetrapods and in teleost fishes ***BUT*** – in one the jaw is very rigid while in the other it is very kinetic.

Fate of the Palatoquadrate, Meckel's Cartilage and the Hyomandibular Arch

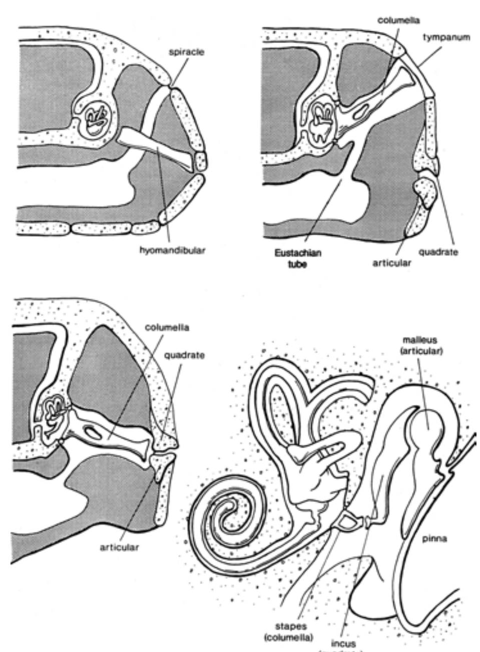


Fig. 45

In all tetrapods, the hyomandibula is reduced to the columella or stapes of the middle ear.

In mammals, the palatoquadrate bone is reduced to the incus of the middle ear plus some cartilage.

In mammals, Meckel's cartilage is reduced to the malleus of the middle ear plus some cartilage.

These changes are thought to reflect two processes. Sound is perceived by structures on the surface of the animal and transmitted via vibration to the middle ear. Initially the hyoid bone attached to the skull in the region of the otic capsule and took on this role. As the jaw suspension changed and the hyoid was no longer needed for attaching the jaw, it became more specialized for its other role. To enhance sound transmission, it became reduced in size (could vibrate better) and shifted its insertion to the thin membrane covering the old spiracular opening (the tympanum).

In the lineage leading to the mammals, with time, the articular bone (old Meckel's cartilage) and quadrate bone (old palatoquadrate) are no longer needed as parts of the jaw. Their removal from the jaw joint was probably the result of changes in feeding style that led to the jaw muscles inserting further forward on the dentary bone, closer to the teeth. As their role in the mechanism of the jaw was reduced, they became reduced in size and slowly dissociated from the jaw to connect to the stapes and assist in sound transmission.

The phylogenetic reduction in size of these bones and their removal from the jaw joint permits their specialization and reduces their mass and increases their oscillatory responsiveness to airborne pressure waves.

Amniote Hyoid
The cerato and basi-hyal elements, along with ventral parts of other anterior pharyngeal arches form the hyoid apparatus that supports the floor of the mouth and the tongue.

Trends

Thus, the chondrocranium (neurocranium) establishes a supportive platform that is joined by contributions from the splanchnocranium. Through phylogenetic progression, the contribution from the splanchnocranium becomes reduced to the hyoid apparatus, the articular, quadrate and hyomandibula. In mammals, these become reduced even further. The dermatocranium encases most of the chondrocranium together with the contributions from the splanchnocranium that remain.

You've looked at skulls in lab and seen the tremendous variation that occurs. Remember:

- Role of the skeleton:
  - Gives the body shape
  - Supports weight (esp. in terrestrial forms)
  - Provides a system of levers that produce movement
  - Protects important tissues

- Role of the skull:
  - Protect the central nervous system
  - Feeding

Almost all adaptations to the skull are for feeding !!!!!