CHAPTER III

DEVELOPMENT OF THE CHONDROCRANIUM

The first indication of the formation of the chondrocranium is noticed in embryos of 4 mm. length, soon after hatching. In an embryo of 3.9 mm. length, (just after hatching) procartilage cells were discernible, but still earlier embryos did not reveal the presence of any cartilage in the head. In embryos of 4 mm. length, the anterior portions of the trabecular cartilages make their first appearance as the sole representative of the chondrocranium. From this stage onwards, development of the embryonic skull steadily progresses on, till in embryos of 6.7 mm. length, the chondrocranium is more or less fully formed and resorption of the cartilages begins. By the time the embryo attains a length of 15.4 mm. stage, further development of cartilage and the resorption of the cartilage is almost complete and the bones of the osteocranium are laid down.

For the purpose of detailed study, the author has selected 13 stages represented by embryos of the following lengths :- (1) 4 mm. (2) 4.1 mm. (3) 4.2 mm (4) 4.4 mm. (5) 4.5 mm. (6) 4.8 mm. (7) 5 mm. (8) 5.2 mm. (9) 5.3 mm. (10) 6.2 mm. (11) 6.7 mm. (12) 10 mm. (13) 15.4 mm. length. Not only an account of the development of the chondrocranium in the above stages have been described in the present work, but a detailed account of the morphology of the chondrocranium and its relation to the blood-vessels, nerves and the eye-muscles have also been given in the case of embryos of 6.7 mm.
and 15.4 mm. lengths. In the description of the chondrocranium, at each stage, a short synopsis enumerating the important features observed is also given in the beginning.

**STAGE 1.** (4 mm. length). Plates 2 to 5 Figs. 2 to 8.

1. The Chondrocranium:

   (a) **Synopsis**:

   Anteriorly, the trabeculae are chondrified but posteriorly they fade away into procartilage. At this stage, the anterior and posterior portions of the parachordals and the auditory capsule are still procartilaginous. The anterior and posterior parachordal procartilages are widely separated off from one another. No trace of the elements of the splanchnocranium appears at this stage.

   (b) **Detailed Account**:

   At this stage, the cartilaginous skull makes its first appearance in the form of a pair of extremely small rod-like cartilages representing the anterior portion of the future trabeculae cranii, confined to the base of the anterior part of the brain, in the eye-region. The trabeculae are distinct from one another and proceed forwards below the brain, one on either side of the mid-ventral line. The front end of each trabecula extends only slightly beyond the tip of the notochord. Posteriorly, however, the trabeculae slightly diverge away from each other and finally end in procartilage.

   The parachordals and the auditory capsules are
procartilaginous at this stage and there is no sign of any chondrification in them as yet. The future anterior and posterior portions of the parachordals chondrify from distinct and independent centres of procartilage cells, which are widely separated from one another at this stage. The anterior portion of the parachordals are in the form of a plate of procartilage located between the notochord and the anterior portion of the otic sac, but distinctly nearer to the median edge of the latter. Posteriorly, however, this plate shows a tendency to approach nearer to the notochord. The auditory capsule is represented by a procartilaginous plate, forming the floor of the anterior portion of the otic sac, beginning a little distance behind its front margin. Posteriorly the procartilage cells of the auditory capsule are directed inwards to become continuous with the procartilage cells of the anterior parachordals. Thus the parachordals and the auditory capsules are in continuity even at the procartilaginous stage. The posterior portion of the parachordals is laid down as a tract of procartilage cells closely adhering to the notochord, on each side, behind the otic sac. At the hinder ends, the procartilaginous cells of the posterior parachordals extend upwards, fore-shadowing the future course of the occipital arches in that region.

As for the splenchnocranium, there is no sign of even the procartilage cells for any of its constituent elements at this stage.

STAGE 2. (4.1 mm. length). Plates 6 to 8 Figs. 9 to 13.

1. The Chondrocranium :
(a) **Synopsis**:

Each trabecula extends further, anteriorly and posteriorly. The front part of the anterior parachordals, the auditory capsule and the anterior basicapsular commissure connecting them are now chondrified at this stage. The anterior parachordals and the trabeculae are now connected by procartilage cells. As for the splanchnocranium, condensation of the procartilage cells appears for the Meckels cartilage and the quadrate in the mandibular arch and the hyosymplectic and the ceratothyyal of the hyoid arch. The Meckels cartilage actually chondrifies for a short length at this stage.

(b) **Detailed Account**:

This stage shows an advancement over the previous stage. The trabeculae show better chondrification and extend slightly more towards the front beyond the tip of the notochord. Each trabecula is rod-shaped, more or less oval in outline in transverse section. Anteriorly the trabecular extremities show a tendency for convergence; but posteriorly they proceed backwards and upwards slantingly to merge into procartilage cells. The procartilage cells of the posterior part of the trabeculae extend at this stage further backwards and become continuous with the procartilage cells of anterior parachordals towards its median edge.

The front portion of the anterior parachordals and the auditory capsule along with their anterior procartilaginous connection, seen in the previous earliest stage as
procartilaginous tracts, have now chondrified. This anterior connection between the anterior parachordals and the auditory capsule forms the anterior basicapsular commissure. The chondrification of the anterior parachordals extend at this stage only for a short length with the result that posteriorly as well as towards its inner extremity, it passes insensibly into procartilage cells. The posterior region of the parachordal approaches nearer to the notochord than its anterior diverging portion. Just behind the otic sac, the procartilage cells for the chondrification of the posterior parachordals (occipital portion) become more extensive and denser than in the earlier stage. They appear thickly clustered and are laid down as continuous sheath of cells, closely attached to either side of the notochord but have not actually chondrified as yet. The procartilage cells of the posterior and the anterior parachordals are still separated off from one another by a wide gap.

In the splanchnocranium, the mandibular arch is represented by a pair of Meckels cartilages which have chondrified for a short length and a pair of quadrates which are represented by procartilage. Anteriorly the two Meckels cartilages converge; but still remain separated from one another by a wide gap. In the hyoid arch, condensation of the mesenchyme cells takes place for the hyomandibular and the symplectic portions of the hyosymplectic and the lower ceratohyal elements. From the very beginning the procartilaginous tracts for the hyomandibular and the ventral symplectic portions appear to be continuous and there is no indication of independent chondrification of these
two portions of the hyosymplectic cartilage from separate centres. Even at this stage, the hyomandibular procartilage has developed a foramen for the exit of the hyomandibular branch of the facial nerve.

**STAGE 3.** (4.2 mm. length) Plates 9 to 12 Figs. 14 to 20.

1. The Chondrocranium:

(a) **Synopsis:**

The trabeculae and the anterior parachordals become continuous with each other. The anterior ends of the trabeculae develop small outwards directed cornu-trabeculae; but the two trabeculae are still widely separated off from each other anteriorly. The posterior parachordals have now chondrified but the rudiments of the occipital arches at their hinder ends are still procartilaginous. In the splanchnocranium, the hyosymplectic cartilage and the ceratohyal show the beginning of chondrification. The ceratobranchials of the first and second branchial arches have also chondrified as small cartilaginous rods.

(b) **Detailed account:**

The anterior parachordals are now fully chondrified and are now in the form of a dorso-ventrally flattened plates of cartilage thicker in the middle and thinner towards their inner and outer ends. Anteriorly, they remain connected on each side with the auditory capsules through the anterior basicapsular commissure. The parachordal plates, progressively get narrower and nearer to the notochord from the anterior to the posterior side. Posteriorly, however, they end
in procartilage cells and are still separated off the notochord by a clear gap. The posterior parachordals now chondrify as thick plates of cartilage on either side of the notochord and are closely attached to it. At this stage, however, these plates soon fade away into the surrounding pro-cartilage cells towards their extremities on all sides except for their mesial side directed against the notochord. At their hinder ends, the procartilage cells proceed outwards and upwards on either side of the brain, thereby laying down the course of development of the future occipital arches.

The auditory capsule remains as a slightly concave plate of cartilage supporting the otic sac from the ventral side.

The trabeculae are more extensively chondrified than in the preceding stage and assume the form of small paired cartilaginous rods. Posteriorly they are relatively flat and plate-like and fuse with the anterior portion of the anterior parachordals. From their point of attachment with the parachordals, they first bend down rather at a sharp angle and then again straighten out proceeding thereafter forwards and downwards slantingly at a level much lower than that of the parachordals. This differential position of the trabeculae and the parachordals is suggestive of a cranial flexure in the early embryo, consequent on its heavily yolked character. In fact, this cranial flexure is characteristic of all such heavily yolked embryos (Norman, 1926). The anterior extremities of the trabeculae develop an outwardly directed process known as the cornu trabeculae.
In the splanchnocranium, the Meckels cartilages elongate further and extend posteriorly nearer to the pro-cartilaginous quadrates. In the hyoid arch, the hyosymplectic cartilage begins to chondrify. The symplectic portion of the hyosymplectic lies in close proximity to the outer limit of the quadrate. The ceratohyal has now chondrified. At this stage, the ceratobranchials of the first and second branchial arches also appear as extremely small paired cartilaginous rods.

**STAGE 4. (4.4 mm. length) Plates 13 to 17 Figs. 21 to 31.**

1. **The Chondrocranium:**
   
   **(a) Synopsis:**

   The anterior and the posterior parachordals are now connected with each other by procartilage cells. The auditory capsule grows backwards behind the anterior basicapsular commissure forming a beginning towards the formation of the outer wall of the basicapsular fenestra.

   In the splanchnocranium, the quadrate has chondrified as a small cartilage. The Meckels cartilage now extends backwards slightly behind the quadrate; anteriorly they converge towards each other and are connected by a mass of pro-cartilaginous cells. In the hyoid arch, the terminal part of the symplectic portion lies close to the outer limit of the quadrate. The third pair of ceratobranchial cartilages also make their appearance at this stage. A small median chondrification representing the copula extends between the 1st and 2nd pair of ceratobranchials.
(b) *Detailed Account*:

All the cartilaginous constituents of the chondrocranium, at this stage, show a better degree of chondrification. The anterior parachordal plates have grown larger due to more extensive chondrification. Posteriorly the parachordals appear to be connected to the notochord by loose procartilage cells towards their inner extremity. The anterior basicapsular commissure connecting the parachordals with the auditory capsule becomes thick and plate-like. Just in front of its anterior margin a shallow concave space is outlined, bordered medially by the anterior portion of the parachordal together with the fused posterior part of the trabecula and laterally by the anterior extension of the auditory capsule. This concave space represents the beginning of the future facial foramen. The posterior parachordals are now more chondrified than in the previous stage with their procartilaginous rudiments of the occipital arches at their hinder ends ascending upwards and outwards on either side of the brain. An interesting feature of this stage is the establishment of a connection between the anterior and posterior parachordals through an intermediary tract of procartilage cells closely adhering to the sides of the notochord, indicating the course of development of the future basal plate of the chondrocranium.

The auditory capsule shows a remarkable growth at this stage. It now grows extending backwards behind the anterior basicapsular commissure as a slightly concave plate of cartilage supporting the otic sac from beneath. Due to this
backward extension of the auditory capsule, a space is enclosed just behind the posterior margin of the anterior basicapsular commissure bounded laterally by the auditory capsule itself and medially by the lateral edge of the parachordals. This space forms the basicapsular fenestra which, at this stage, is not complete but open posteriorly. Anteriorly, the auditory capsule now extends forward up to the anterior limit of the otic sac. Even at this stage the foundation for the future posterior basicapsular commissure is seen laid out as a strand of procartilage cells stretching transversely between the procartilage cells flanking the notochord and the otic sac towards its posterior region.

Anteriorly, the trabeculae now show a tendency to approach each other. The cornu trabeculae become more pronounced than in the previous stage.

In the splanchnocranium, the various cartilaginous elements are comparatively better chondrified. In the mandibular arch the quadrate condifies now as a small cartilage towards the inner side of the symplectic portion of the hyosymplectic cartilage. The Heckel's cartilage, in the lower jaw, is more elongated and posteriorly approaches nearer to the quadrate and extends slightly behind it; but both remain quite separate and no contact, whatsoever, is established between the two. Anteriorly the Heckel's cartilages are still connected with each other by a mass of procartilaginous cells. The broad base of hyomandibular portion of the hyosymplectic articulates with the ventro-lateral region of the auditory capsule and lower down the foramen for the transit of the
hyomandibular branch of the facial nerve become more prominent. The ceratohyal is in the form of a small rod of cartilage running obliquely towards the median line, one on each side. A procartilaginous stylohyal appears now. In the branchial arches, the third pair of ceratobranchials have chondrified and all the three pairs of ceratobranchials are in the form of small rods of cartilage which are rather obliquely disposed on either side of the mid-ventral line. A small median copula also chondrifies at this stage in mid-ventral line and extends in between the 1st and 2nd pair of ceratobranchials.

STAGE 5. (4.5 mm. length) Plates 18 to 21 Figs. 32 to 41.

1. The Chondrocranium :

(a) Synopsis :

The parachordals now form a continuous cartilage lying on either side of the notochord. The conspicuous occipital arches extend further upwards. Anteriorly the base of the auditory capsule now extends up to the anterior most limit of the otic sac and small pro-otic process appears at its anterior margin. Anteriorly the trabeculae fuse together to form an ethmoid plate.

In the splanchnocranium, the quadrate develops a miniature pterygoid process dorsally towards its anterior portion. The Meckels cartilage articulates with the quadrate posteriorly giving out still behind a small retro-articular process. In the hyoid arch, a stylohyal and a median hypohyal chondrify independently, on each side. In the branchial arches, first two pairs of hypobranchials and the
fourth pair of ceratobranchials appear now.

(b) Detailed Account:

At this stage extensive chondrification of the anterior and posterior parachordals takes place including the intervening zone of procartilaginous connection between them, forming thereby a continuous and elongated dorso-ventrally flattened plate of cartilage, the hinder portion of which is closely applied to the sides of the notochord. This constitutes the basal plate of the chondrocranium which appears for the first time at this stage as a fully developed and continuous structure. The anterior part of the parachordals diverge away from the notochord leaving a small space between them and the anterior end of the notochord. This space represents the basicranial fenestra which at this stage is confluent anteriorly with the posterior part of the hypophysial fenestra.

The anterior margin of the auditory capsule now extends forward upto the anterior limit of the otic sac and is produced antero-laterally into a small post-orbital process.

The converging anterior portions of the trabeculae now fuse together forming the ethmoid plate which is the sole representative of a cartilaginous floor in the ethmoid region. With the formation of the ethmoid plate, the hypophysial fenestra is complete anteriorly, though posteriorly it is still confluent with the basicranial fenestra. The ethmoid plate is
broadest towards the front, progressively getting narrower towards its posterior region where it is continued further backwards as the paired trabeculae. The trabeculae at this stage exhibit a decrease in the degree of their downward flexure.

In the splanchnocranium also, this stage shows advancement over the previous stage. In the mandibular arch, the quadrate gives out a small pterygoid process dorsally towards the anterior side. This process is distinguished by its thin plate-like structure from the thick quadrate portion. Anteriorly, the Meckels cartilages, now fuse with each other forming a median symphysis; posteriorly, each Meckels cartilage now articulates with the quadrate along its ventral portion. Behind the point of articulation, the Meckels cartilage is produced backwards as a small blunt retro-articular process. In the hyoid arch, the stylohyal now condrifies independently as a somewhat dorso-ventrally compressed piece of cartilage connecting the hyosymplectic cartilage with the posterodorsal portion of the ceratohyal. The ceratohyals are now well developed. The hypohyal develops as an independent condrification towards the median extremity of the ceratohyal. The broad base of the hyomandibular articulates by a flat surface with the ventro-lateral surface of the auditory capsule. The symplectic portion now grows slantingly forwards and downwards and its terminal portion comes to lie just below the quadrate, giving a slight support to this small and almost vertically disposed cartilage from beneath. Both the cartilages, however, remain quite distinct and do not become fused with each other.
Medially to the first and second pair of ceratobranchials, the first and second pair of hypobranchials now chondrify from independent centres, as small cartilages lying on either side of the median copula. The fourth pair of ceratobranchials also appears at this stage as a small rod of cartilage. The median copula elongates backwards and now extends up to the third pair of ceratobranchials. The small hyobranchials still remain separate from the copula as well as from the corresponding ceratobranchials.

STAGE 6. (4.8 mm. length) Plates 22 to 27 Figs. 42 to 54.

1. **The Chondrocranium**

   (a) **Synopsis**:

   Posteriorly, the occipital arches fuse with the posterior extremity of the medial wall of the auditory capsules enclosing the fissura metotica for the passage of the vagus nerve. Anteriorly the parachordal develops a post-palatine process which, however, is still not fused with the developing pro-otic process of the auditory capsule. The posterior basicapsular commissure develops behind the exit of the glossopharyngeal nerve and thus the basicapsular fenestra is now completely formed. In the splanchnocranium, the quadrate develops posteriorly a metapterygoid and a diminutive otic process directed towards the auditory capsule. In the branchial arches, the 5th pair of ceratobranchials also appear at this stage as small rods of cartilage; the third pair of hyobranchials also chondrify at this stage. A second small piece of copula appears posterior to the first one. The fused 3rd and 4th pharyngo-branchials
appear dorsally as an irregularly shaped plate of cartilage.

(b) **Detailed Account**:

The basal plate has further grown in size and the occipital arches now extend up to the posterior limit of the auditory capsules and their dorso-lateral portions fuse with the posterior extremity of the median wall (septum of the posterior semicircular canal) of the auditory capsules leaving a passage known as the fissura metotica, between the occipital arch and the auditory capsule, through which the vagus nerve leaves the skull. Towards the anterior region, the anterior portion of the parachordal develops slightly beyond the concavity destined to be the future facial foramen and gives off a post-palatine process which proceeds outwards and forwards towards the inwardly growing pro-otic process from the auditory capsule. These processes represent the fore-runners of the future lateral commissure (formed by their further approach and fusion) in later stages, which completes the facial foramen.

The auditory capsule shows further development at this stage and its lateral border extends upwards especially in the anterior and middle regions. Inside, the three semicircular canals of the membranous labyrinth (the anterior, lateral and the posterior) can be well-marked out and the cartilaginous septa enclosing them are in the process of formation. The septum of the posterior semicircular canal is comparatively better developed than the others and dips downwards and Inwards
to fuse with the occipital arch posteriorly, as already mentioned before. Another feature of interest at this stage is the development of a transverse posterior basicapsular commissure towards the posterior region of the auditory capsule, which becomes fused with the corresponding parachordal. As a result of the development of this commissure, the basicapsular fenestra becomes enclosed by cartilage on all sides. This posterior basicapsular commissure is formed clearly behind the exit of the glosso-pharyngeal nerve, which henceforth leaves the skull through the posterior region of the basicapsular fenestra.

The anterior portion of the trabeculae just behind the ethmoid plate fuse together for a very short length, forming a small trabecula communis. The place where posterior portion of the paired trabeculae cranii and the anterior parachordal processes fuse with one another is slightly depressed and hence lies at a somewhat lower level than the rest of the basal plate and the anterior part of the trabeculae.

In the splanchnocranium, in the mandibular arch, the pterygoid portion arising dorsally from the quadrate shows further growth and has advanced further forwards towards the ethmoid plate, as a small rod-shaped cartilage. The quadrate has grown further and gives out a conspicuous, laterally compressed plate-like metapterygoid process bearing a small otic process from its hinder end. This entire posterior section of the quadrate proceeds postero-dorsally towards the auditory capsule, resting on the forwardly directed slanting rod-like symplectic portion of the hyosymplectic cartilage, and receiving support from it. Ventrally the quadrate, at about its point of union with the
pterygoid portion in front, gives off a small articular process, which articulates with the posterior part of the Meckels cartilage. The Meckels cartilage has grown further in length; posteriorly, behind the point of its articulation with the quadrate, its retro-articular process has slightly increased in size. In the hyoid arch, all the four cartilaginous elements are well developed. The large hyomandibular portion is more or less triangular in form, attached to the ventro-lateral region of the auditory capsule by its broad base. The narrower apex is continued imperceptibly into the symplectic portion which now appears as a well-developed tapering rod of cartilage extending downwards and forwards lying in close association with the postero-ventral margin of the quadrate and giving support to it. The large ceratohyal maintains its connection with the postero-ventral part of the hyosymplectic cartilage through a small interhyal cartilage. The hypohyals become larger and approach close together towards the mid-ventral line. In the branchial arches, the 5th pair of ceratobranchials appear as a pair of small rod-like cartilages behind the fourth pair. All the five pairs of ceratobranchials are placed obliquely backwards and outwards from the mid-ventral line. Another feature of interest in the branchial skeleton is the appearance of an irregularly shaped plate of cartilage dorsally towards the mesial side of the third and fourth ceratobranchials. This plate represents the fused third and fourth pharyngobranchials. The anterior median copula becomes longer and now extends between the first three pairs of ceratobranchials. A short posterior copula now chondrifies independently.
behind the first one and lies between the proximal portion of
the third pair of ceratobranchials and extends backwards up to
the next or the fourth pair of ceratobranchials.

STAGE 7. (5mm. length) Plates 28 to 32 Figs. 55 to 65.

1. The Chondrocranium:

(a) Synopsis:

At this stage the post-palatine process of the para-
chordal and the pro-otic process of the auditory capsule unite
and fuse with each other to form the lateral commissure forming
the lateral wall of the trigeminofacialis chamber. The carti-
laginous auditory capsule now extends well up the lateral sides
of the otic sac. The post-orbital process of the auditory
capsule becomes well marked. The basicapsular fenestra gets fur-
ther reduced in size due to further chondrification and extension
of the floor of the auditory capsule. The basicapsular fenestra
gets divided into a smaller anterior and a larger posterior
portion due to the formation of a bridge of cartilage across it.
The ethmoid plate develops now a small ridge which marks the
beginning of an internasal septum. The trabacula communis has
further increased in length posteriorly. The orbital cartilage
appears at this stage as a small rod of cartilage on each side,
independently of other cartilages and is not attached to any other
cartilage.

In the splanchnocranium, each Meckels cartilage
immediately in front of its articulation with the quadrate develops
a small coronoid process. In the hyoid arch, a small rudimentary
basihyal appears as an independently chondrified piece of cartilage. The second pharyngobranchial cartilage makes its appearance at this stage and so do the first and second epibranchials also.

(b) Detailed Account:

At this stage, the post-palatine process of the parachordal and the corresponding pre-otic process of the auditory capsule, which were growing towards each other in the earlier stage, meet and unite to form a bridge of cartilage known as the lateral commissure which lies ventral and lateral to the head vein. The lateral commissure forms the lateral wall of a small trigemino-facialis chamber which opens behind by the facial foramen. The sides of the auditory capsule now extend well up the lateral sides of the otic sac and in the anterior portion the lateral wall is almost complete, but towards the posterior side it is incomplete and what little of the cartilage extends into this region by way of a lateral wall passes insensibly further up into procartilage cells. In the region of the posterior semicircular canal, only the cartilaginous floor exists, and the lateral wall is non-existent. The floor of the auditory capsule now extends far back up to the posterior limit of the otic sac. The basi-vestibular fenestra gets further reduced in size due to further growth of cartilage and the single large basi-vestibular fenestra of earlier stages becomes divided into a small anterior and a large posterior one by the formation of a bridge of cartilage across it.

Anteriorly the ethmoid plate has grown into a relatively thicker and broader plate of cartilage and along its
The mid-dorsal line in its anterior portion, develops a low vertical ridge which indicates the beginning of the internasal septum. Posteriorly, behind the ethmoid plate, the fusion and formation of the trabecula communis extends further back at this stage, so that the trabacula communis extends further backwards. Posteriorly to the trabecula communis, the paired trabeculae cranii remain distinct and run backwards bordering the hypophysial fenestra laterally to fuse with the anterior parachordal processes on either side. The most striking feature of this stage is the first appearance of the orbital cartilages, which appear as small paired rods of cartilage in the dorso-lateral region between the fore-brain and the orbit, one on each side. These orbital cartilages arise independently of other cartilages and are placed nearer to the ethmoid than to the auditory region. Both anteriorly as well as posteriorly, the orbital cartilages are prolonged into procartilage.

In the splanchnocranium, the pterygoid portion of the quadrate has grown further forwards and now reaches almost up to the posterior limit of the ethmoid plate. The Meckels cartilage of the lower jaw elongates further and now reaches up to a level just behind the anterior margin of the ethmoid plate. Anteriorly, the two Meckels cartilages meet in the mid-ventral line in a symphysis which is now well marked by the presence of a median groove. Posteriorly, each Meckels cartilage becomes thicker towards the point of its articulation with the quadrate and a little ahead of this articulation, gives out a short, blunt coronoid process.
In the hyoid arch, the two hypohyals have approached close to the median line; but they still remain distinct from each other. A median and unpaired small basihyal makes its appearance as an independent chondrification just in front of the two hypohyals. Its posterior terminal portion extends dorsally in between the hypohyals with which it appears to be connected by procartilage cells. In the branchial arches, all the five pairs of ceratobranchials are well developed. The hypobranchials are well developed in the first three branchial arches and remain closely articulated with the median edge of the respective ceratobranchials. As for the dorsal elements, the plate-like fused third and fourth pharyngo-branchial, observed in the preceding stage, has increased in size and anterior to it the second pharyngo-branchial chondrifies from an independent centre, as a small nodule-like cartilage, mesially to the second epibranchial. The epibranchials also of the first two branchial arches make their appearance as independent chondrifications dorsally towards the proximal ends of the respective ceratobranchials. The first pair of epibranchials are better developed than the second pair. Both these pairs of epibranchials do not actually articulate with the ceratobranchials concerned, but remain separated by a mass of procartilage cells. Of the two median copulas, the anterior one has extended further backwards now stretching longitudinally from behind the two hypohyals up to the third pair of hypobranchials. The posterior copula has also grown in length and anteriorly it reaches forward almost up to the posterior extremity of the first copula.
STAGE 8. (5.2 mm. length) Plate 33. Figs. 66 to 68.

1. The Chondrocranium:

(a) Synopsis:

In the basal plate the anterior basicapsular fenestra has become further reduced in size. In the posterior region of the auditory capsule, there is a tendency for the lateral wall just to arch over the cranial cavity, but as yet a cartilaginous roof in the region is not developed. A cartilaginous septum for the lateral semicircular canal also condries now. The internasal septum is now well differentiated and is continued upwards into procartilage cells. The two orbital cartilages are now produced towards the mid-dorsal line into epiphysial processes which, however, do not unite with one another at this stage. Posteriorly, the orbital cartilages are connected with the corresponding post-orbital process of the auditory capsule by a bar of pro-cartilage.

In the splanchnocranium, the retro-articular process and the coronoid process of Meckel's cartilage are now well pronounced. The epibranchials of the third and fourth branchial arches appear at this stage but that of the third arch is still represented by procartilage. The first and second pair of hypobranchials now become attached to the anterior copula.

(b) Detailed Account:

The chondrocranium shows a general increase in size due to the continued growth and more complete chondrification of its
already existing cartilaginous constituents. The parachordal plate has increased in length. The auditory capsule shows relatively better development. In the anterior portion the lateral wall is complete and well chondrified ending free dorsally. Towards the more posterior region, there appears to be a pronounced tendency on the part of the dorsal portion of the lateral wall to arch over and extend towards the roof, where it merges into procartilage cells. However, there is still no sign of a cartilaginous roof in this part of the auditory region, since what little advance has been made in the direction of the roof is represented by procartilage cells only. In the region of the posterior semicircular canal, the floor as well as the lateral wall is much better developed, when their condition in the earlier stage is recalled. The cartilaginous septum for the lateral semicircular canal makes its first appearance, at this stage, replacing the early membranous septum. The floor of the auditory capsule is more chondrified with the result that the two basicapsular fenestrae get further reduced in size.

The ethmoid plate is quite well-developed and prominent. The incipient ridge of cartilage representing the beginning of the internasal septum, observed in the previous stage, has grown further in size. It now projects up as a vertical cartilaginous ridge of cartilage from the mid-dorsal region of the ethmoid plate and is continued upwards into procartilage cells. This median septum, however, is still in the process of formation and at this stage is confined to a short distance in the anterior part of the ethmoid plate,
fading away posteriorly, where the dorsal part of the ethmoid plate is occupied by the anterior extension of the brain.

Behind the ethmoid plate the trabecula communis extends further backwards bringing about a corresponding reduction of the hypophysial fenestra. The notochord begins to show a tendency to recede backwards and at this stage its anterior tip now does not extend forward beyond the level of the facial foramen.

The extremely small rod of orbital cartilage, observed in the previous stage, shows remarkable development now. It has grown much larger in size. It becomes progressively thicker from the anterior to the posterior portion and develops an inwardly growing cartilaginous epiphysial process which proceed slightly upwards arching over the dorsal portion of the fore-brain towards the fellow of the opposite side. But at this stage they do not meet one another, but are separated by a gap of procartilage cells.

Behind the epiphysial process, the orbital cartilage proceed further back for a very short distance and are continued into a dense tract of procartilage cells which extend backwards upto the post-orbital process of the auditory capsule.

In the splanchnocranium, no major changes are noticed except for the fact that both the third and fourth epibranchials make their appearance, though the third one is still represented by procartilage. The pterygoid portion of the quadrate runs obliquely forwards and upwards as a rod-like cartilage below the
trabecula communis and extends anteriorly up to the middle of the ethmoid plate. Its anterior tip lies immediately below the ventro-lateral region of the ethmoid plate, and is separated from the latter by a small gap. In the lower jaw, the Meckels cartilage elongates further and extends forwards slightly beyond the pterygoid portion reaching almost upto the anterior margin of the ethmoid plate. Anteriorly, the extremities of both the Meckels cartilages are somewhat thickened and meet each other in the median synphysis, which is indicated by the prominent groove. The retro-articular and the coronoid processes of the Meckel's cartilages are more pronounced at this stage. In the hyoid arch, the median basihyal has become enlarged into a dorsoventrally compressed plate-like cartilage, more or less triangular in shape and projecting forwards just in front of the two large hypohyals. The posterior narrower rod-like portion now extends further backwards dorsally in between the two hypohyals and reaches upto the commencement of the anterior copula, where it remains in procartilaginous connection with the latter as well as with the hypohyals. The last plate-like pharyngobranchial representing the fused third and fourth pharyngobranchials, shows a marked increase in size and shifts backwards so that its proximal portion comes to lie in close proximity to both the third and fourth epibranchial cartilages. The third and fourth epibranchial elements now chondrify dorsally from independent centres near the proximal ends of the corresponding ceratobranchials as new additions to the branchial arch skeleton. The fourth epibranchial is a small chondrified element, but the third one is smaller and is
still in the process of chondrification, being mostly procartilaginous in character. The first epibranchial now develops into an expanded blade-like cartilage, whose broad distal margin is bifurcated roughly into two portions by a very shallow concavity or notch. The fifth ceratobranchial has developed into a long and comparatively slender cartilaginous rod. Its anterior portion more or less runs parallel to the median line in close association with its fellow of the opposite side; but posteriorly it diverges away from it. An interesting feature of this stage is that the first and second pairs of hypobranchials get closely applied to the sides of the anterior copula. The second copula still remains separated from the anterior copula by an intervening gap and extends backwards up to the level of the fourth pair of ceratobranchials.

STAGE 9. (5.3 mm. length) Plates 34 to 35 Figs. 69 to 74

1. The Chondrocranium:

(a) Synopsis:

In the hinder region, the roof of the auditory capsules are produced inwards to form well-developed synotic processes. Anteriorly, the epiphysial processes of the orbital cartilages have fused with one another over the roof of the cranial cavity to form a slender epiphysial cartilage. Posteriorly, the orbital cartilages extend backwards and fuse with the postorbital processes of the auditory capsules.

In the splanchnocranium, the basihyal extends backwards
and covers the tip of the anterior copula for a very short distance, the two being connected by procartilaginous cells. The third epibranchial has now fully chondrified.

(b) **Detailed Account**:

Except for the following features of interest, the chondrocranium, at this stage, shows more or less in the same condition as in the preceding stage. In the auditory region, the posterior basicapsular fenestra gets further reduced due to further in-growth of the cartilaginous floor surrounding it. In the hinder region, the wall of the auditory capsule arches over dorsally to form a synotic process over the roof of the cranial cavity.

In the orbito-temporal region, the epiphysial processes of the orbital cartilages grow further inwards and fuse with each other completing the formation of a transverse epiphysial cartilage which forms part of the roof of the cranial cavity. Anteriorly to the epiphysial bar, the orbital cartilage extends forward for a short distance as a slender cartilaginous rod; but posteriorly it extends backwards to fuse with the post-orbital process of the auditory capsule, on each side, to form the taenia marginalis. It is of interest to note that, in a other embryo of about the same length, this connection of the posterior part of the taenia marginalis with the auditory capsule is seen established, even prior to the complete formation of the epiphysial bar anteriorly.

The splanchnocranium remains almost the same as in the previous stage. The Meckels cartilages of the lower jaw, however, now extend forward even beyond the level of the ethmoid plate. The posterior narrower rod-like portion of the basihyal extends
further back and now overlaps the anterior extremity of the first copula for a very short length and the two cartilages, in this region, are closely connected with each other through surrounding procartilage cells. The third epibranchial has fully chondrified at this stage.

STAGE 10. (6.2 mm. length) Plates 36 to 41 Figs. 75 to 87.

1. The Chondrocranium:

(a) Synopsis:

At this stage, the auditory capsule has fully chondrified, with well developed floor, lateral wall and roof. In its hinder region, the synotic processes of the two sides now fuse with one another along the mid-dorsal line forming a complete tectum synoticum. The anterior basicapsular fenestra is completely obliterated on the right side, but persists on the left side. The posterior basicapsular fenestrae are further reduced in size, but the glossopharyngeal nerve still passes out of the cranium through it.

Anteriorly, the orbital cartilages extend forward up to the ethmoid plate and are produced inwards into sphenoseptal commissures which fuse with the internasal septum. The postero-lateral margin of the ethmoid plate is produced outwards and upwards on each side to form a small lamina orbitonasalis.

In the splanchnocranium, anteriorly, the pterygoid portion lies in close contact with the ventro-lateral region of the ethmoid plate, but an ethmopalatino process of the ethmoid plate
is absent. The anterior and posterior copula are now in contact with each other. The third pair of hypobranchials are now attached to the sides of the copula. All the four pairs of epibranchials now articulate with the corresponding cerato-branchials.

b) Detailed Account:

The chondrocranium, as a whole, has become more compact and the various cartilaginous elements constituting it have almost attained the condition found in the fully developed embryonic skull, just prior to the initiation of the absorption of cartilages. The parachordals are in the form of broad plates of cartilage adpressed to the sides of the notochord posteriorly. Anteriorly, the parachordals diverge away from the notochord, leaving a narrow basicranial fenestra, which is confluent in front with the hypophysial fenestra. More posteriorly the median portion of the parachordals just adjacent to the notochord, on each side, is relatively much thicker and distended and together with the notochord, present a somewhat elevated or convex median structure, flanked on either side by a large trough-like shallow depression which lodges the downward and inward extensions of the saccule of the membranous labyrinth. This portion of the parachordal supporting the saccule from beneath, is extremely thin. However, immediately behind this depression, the parachordal again becomes uniform in its thickness.

The auditory capsule is now fully chondrified and completely encloses the auditory sac. The posterior semicircular
canal also is now provided with, besides the well developed floor, a cartilaginous lateral wall and roof, which were rather incomplete in the earlier stage. In the hinder portion, the roof of the auditory capsule extending up the dorso-lateral regions of the brain (the synotic process of the previous stage) grows further to meet and fuse with its fellow of the opposite side to form a complete tectum synoticum. This tectum synoticum constitutes a posterior roof to the chondrocranium in the auditory region. Due to further chondrification of the floor of the auditory capsule, the posterior basicapsular foramen for the exit of the glossopharyngeal nerve become further reduced in size, and the anterior basicapsular fenestra becomes obliterated completely on the right side, though it persists as a small fenestra on the left side.

Anteriorly the ethmoid region shows a remarkable advance over the preceding stage. The ethmoid plate is very well developed and the internasal septum projects vertically up from its mid-dorsal line as a thick median ridge. It extends more posteriorly than in the earlier stage. The posterolateral margins of the ethmoid plate are produced upwards and outwards into small processes known as the lamina orbitonasalis or ectethmoid cartilages. The ethmoid plate is continued posteriorly into an extensive trabecula communis, surmounted by a well developed membranous inter-orbital septum, limiting the base of the brain cavity above. The *trabecula communis*, characteristic of a triptitrabic chondrocranium, now stretches far back up to the anterior limit of the much reduced hypophysial fenestra, just a short distance in front of the place of approximation of the
floor of the brain cavity with the floor of the neurocranium. Towards the posterior portion of the trabecula communis, the transverse bridge-like dorsal cartilaginous connection between the diverging ends of the trabeculae arches and shows a tendency to grow upwards in the place of the membranous inter-orbital septum, just after which the paired trabeculae separate from it and proceed divergingly backwards fringing the lateral sides of the hypophysial fenestra. This arched bridge of cartilage, representing an extension of dorsal portion of the posterior extremity of the trabecula communis, marks the beginning of the future cartilaginous inter-orbital septum, which is confined to the posterior portion of the orbital region, in later stages.

The anterior part of the orbital cartilage, beyond the epiphysial bar, now extends forward into the ethmoid region, where it gets slightly expanded and develops an inwardly directed sphenoseptal commissure which fuses with the posterior portion of the internasal septum forming the posterior border of the roof of the olfactory foramen in this region. The middle portion of the epiphysial cartilage is now much wider than in the previous stage.

Except for the first pair of pharyngobranchials, the full compliment of the fully formed cartilaginous splanchnocranium is present now. In the ethmoid region the anterior portion of the pterygoid section of the upper jaw comes in close contact with the ventro-lateral region of the ethmoid plate and thus articulates with it. This articulation conforms
to the posterior ethmopalatine articulation of other fishes. Beyond this articulation, the anterior portion of the pterygoid bar is again separated off from the ethmoid plate and extends forwards for a very short distance only. The quadrate section is very well marked with a large thick plate-like metapterygoid portion bearing the rudimentary otic process at its terminal end directed towards the auditory capsule; but the latter fails to reach the auditory capsule as is the case in teleosts, in general. In the lower jaw, the coronoid and the retroarticular processes of the Meckel's cartilages have become more prominent than in the preceding stage. In the hyoid arch, the distal rounded portion of the ceratohyal now fits into a concavity of the proximal part of the hypophyal, thus fore-shadowing the typical "ball and socket" articulation between these two cartilages. The plate-like anterior portion of the basihyal has very much expanded forwards in front of the hypohyals. Both the anterior and posterior copulae are now in contact with each other and the third pair of hypobranchials articulate with both the copulae at their place of junction.

Regarding the branchial arches, the second pharyngo-branchial has grown into a heart-shaped structure. The last pharyngo-branchial has still further increased in size and the two small nodule-like projections towards their anterior margins, observed in the previous stage, have developed into well defined horn-like processes directed forwards. The notch at the distal margin of the first epibranchial gets deeper and its bifurcation becomes more conspicuous. All the epibranchials now get articulated with corresponding ceratobranchials.
STAGE 11 (6.7 mm. length) Plates 42 to 61 Figs. 88 to 123

The Chondrocranium:

(a) Synopsis:

This stage shows the beginning of the absorption of cartilage of the neurocranium and a break occurs between the trabacula eranii and the corresponding parachordal. A short distance behind the anterior end of the notochord, the latter becomes roofed over by a narrow prootic bridge connecting the two parachordals. At this stage, the tectum synoticum has greatly increased in width and forms a roof over the greater part of the auditory region. In the ethmoid region, the lamina orbitonasalis or ectethmoid cartilage becomes fused with the sphenethmoid process of the orbital bar to form a sphenethmoid commissure. A small rostral cartilage also appears in the median line just anterior to the ethmoid plate.

The short trabecula joining the anterior parachordal process with the more anterior trabecula communis is reduced to an extremely thin rod of cartilage (due to partial absorption of cartilage already set in.) on one side, whereas on the other side in the same embryo, it has been completely absorbed.

In the splanchnocranium, the ceratohyal increases in size and posteriorly forms a blade-like expansion. The first pharyngobranchial makes its appearance at this stage.
The two horns of the fused third and fourth pharyngobranchials \textit{makin} get completely detached from the parent cartilage due to the absorption of intervening cartilage and these pieces get attached to the second pharyngobranchials.

(b) \textit{Detailed account}:

The chondrocranium attains its full development now, the full complement of its cartilaginous constituents being present at this stage, except the epichordal commissure which develops later. This stage also shows the beginning of the absorption of some of the already formed cartilages of the chondrocranium. At this stage, the two parachordals are connected with one another anteriorly by a slightly arched bridge or shelf of cartilage known as the pro-otic bridge which is situated a short distance behind the anterior tip of notochord. Its slightly concave ventral margin is closely apposed to the dorsal side of the notochord, leaving practically no space in between them. The ventro-lateral portions of the medial edges of the parachordals, however, are free and the narrow channel-like space between them and the notochord represents the intramural section of the posterior myodome. At this stage, the beginning of the epichordal commissure is also seen. This is represented by the epichordal processes which arise from the hinder region of the parachordals, one on either side, which curve over the notochord dorsally.

The tectum synoticum has grown further and now covers the greater part of the roof of the brain cavity in the hinder region of the neurocranium. Its posterior margin is produced
backwards into a short knob-like structure which extends dorsally between the two occipital arches.

Anteriorly the ethmoid region shows better development at this stage. The ethmoid plate and the internasal septum projecting up vertically from its dorsal surface is very well pronounced. The prominent posterior portion of the septum develops a shallow concavity on its dorsal side, immediately after which the sphenoseptal commissures of the orbital cartilages on either side fuse with it. The nasal fossa is now provided with a floor formed by the lateral expansion of the ethmoid plate, a median wall formed by the internasal septum and a lateral and hind wall formed by the lamina orbitonasalis. The lamina orbitonasalis is now a laterally compressed plate-like structure, rising vertically up and fuse with the well chondrified short sphenethmoid commissure of the orbital cartilage, thus establishing a cartilaginous lateral wall to the posterior portion of the nasal fossa for the first time. A roof to the nasal capsule is non-existent except in its hindermost region, where the sphenoseptal commissure forms the dorsal wall of a wide foramen olfactorium adhehens through which the olfactory nerve, the orbitonasal artery and orbitonasal vein, pass from the orbital cavity into the nasal fossa. Immediately in front of the ethmoid plate, a small independent rostral cartilage appears as an additional structure.

Behind the ethmoid plate, the trabecula communis become still more extensive and attains its maximum development.
The rudiment of the cartilaginous inter-orbital septum shows slightly better development in comparison with the preceding stage. At first the trabaculae cranii taper posteriorly to a slender point where they join the corresponding parachordals due to the absorption of cartilage and eventually a break occurs at this point in the connection between the two cartilages. As a rule, the break occurs first on one side but it is soon followed on the other side. Thus in some cases the break may be seen to be complete only on one side. The middle portion of the epiphysial cartilage now becomes much wider than in the previous stage. Anteriorly, in the ethmoid region the sphenethmoid commissure has chondrified at this stage and fuses with the upgrowing lamina orbitonasalis, completing the lateral wall of the nasal fossa in this posterior region.

The splanchnocranium now fully developed as the first pharyngobranchials are also formed at this stage. In the hyoid arch, the hinder portion of the ceratohyal develops into a broad laterally compressed blade-like structure. Anteriorly, the rounded terminal portion of the ceratohyal fits into a deep concave cup-like depression formed at the posterior margin of the hypohyal forming a 'ball and socket' joint. The two well developed horns of the fused third and fourth pharyngobranchials, observed in the previous stage, now get completely detached from the parent cartilage due to absorption of interveing cartilage and become attached to the posterior margin of the second pharyngobranchial in front, as small round pieces of cartilage. Resorption of cartilage followed by ossification is already noticeable at this stage in the case of the fifth pair of cerato-branchials where it occurs along the middle portion with the
result that the cartilage is now confined to its anterior and posterior portions only with bony formation in between. The cartilaginous outgrowths given out by the third hypobranchials, which extend forward on either side of the first copula posteriorly, are very conspicuous at this stage and bend down to partially enclose the ventral aorta, on either side.

Thus at this stage, the first three pairs of branchial arches are provided with the complete set of cartilaginous elements, which make up a typical teleostean branchial arch, the fourth pair being devoid of the ventral hypobranchial elements. The fifth arch is represented only by the ceretobranchials.

Out of the median elements, the basihyal and the first and second copulae are all joined with one another at their extremities by the intervening procartilage cells. The anterior portion of the first copula overlaps the posterior portion of the basihyal for a short length, where the two are joined to each other; similarly the posterior portion of the first copula overlaps the anterior tip of the second copula at their place of association.
STAGE 12. (10 mm. length) Plates 62 to 68 Figs. 124 to 133.

1. The Chondrocranium:

(a) Synopsis:

At this stage, the posterior myodome is now complete with the addition of the posterior sub-cranial section. An epichordal commissure passing over the notochord and connecting the two paraphyseals posteriorly also makes its appearance at this stage. The absorption of cartilage in the dorsal and lateral wall of the auditory capsule extends further and the vacuities so created are bordered by the developing otic bones.

The lamina orbitonasalis extends further forwards and takes part in the formation of the lateral wall of the olfactory fossa. The orbital cartilage also extends further forward and takes part in the formation of the roof of the olfactory fossa in the hinder region. The trabacula communis is further reduced in length due to the absorption of cartilage posteriorly and due to this, a small inter-orbital septum now separates off as an independent piece of cartilage. The epiphysial cartilage becomes broader and is produced backwards into a taenia tecti mediales.

Detailed Account:

The chondrocranium has considerably increased in size and absorption of the existing cartilages, initiated at 6.7 mm. stage, has made further progress and a number cartilage as well as membrane bones make their appearance
at this stage.

In the region of the basal plate, the prootic bridge connecting the anterior portion of the parachordals above the notochord has become more extensive and is now in the form of a thick arched shelf of cartilage forming a more complete roof over the intra-mural section of the posterior myodome. The posterior myodome is very well developed at this stage and has all the three sections i.e., the anterior or intra-cranial, the middle or the intramural and the posterior or sub-cranial sections. The last one is an addition at this stage due to further backward growth and elongation of the external rectus eye-muscle. The sub-cranial section extends backwards behind the posterior limit of the prootic bridge, where the terminal portions of posterior rectus eye-muscles are lodged in the concave space or groove beneath the convex surface formed by the distended and slightly upturned medial portions of the parachordals. This concave space underneath the parachordals forms the last sub-cranial section of the posterior myodome. In the region of the prootic bridge, the posterior myodome forms an inverted gutter-like channel roofed over by the prootic bridge; its sides are formed by the downward extensions of the free median edges of the two parachordals. The external and internal rectii eye-muscles are lodged in this myodome in separate compartments separated by membranous partitions.

The noteworthy feature of this stage is the first appearance of an epichordal commissure bridging over the notochord at the hinder ends of the two parachordals, in the
occipital region, by the further upward growth and fusion of the small epichordal processes which were discernable even in the previous stage. There is complete absorption of the paired trabeculae and an appreciable portion of the posterior part of the trabecula communis has also been absorbed so that the latter has decreased considerably in length.

Compared with the earlier stage, extensive absorption of the cartilage has taken place in the region of the auditory capsule; simultaneously ossification also sets in this region. Anteriorly, due to the formation of a large prootic bone, the ossification has spread over the anterior lateral commissure and extends backwards over the cartilage fringing the facial foramen in the wake of the absorption of the cartilage in the region. Thus the facial foramen is now surrounded by the developing prootic bone. Behind the prootic bone, the floor of the auditory capsule develops two more vacuities, due to the absorption of the cartilage; the anterior one is somewhat lateral to the posterior portion of the prootic bone while the posterior one is in the posterior part of the parachordal plate which lodges the saccular extension of the membranous labyrinth. The small anterior basicapsular fenestra, observed on one side only in the earlier stage, becomes obliterated by the backward extension of the ossification and formation of the prootic bone. The ossification of the lateral commissure takes place in the form of an inner and outer lamellae with the absorption of the cartilage in between them. Due to the formation of these two lamellae, the trigeminofacialis chamber now gets partitioned into an upper pars
ganglionicus, limited medially by the dura mater and externally by the inner lamella, and a lower pars jugularis occupying the space between the two lamellae. The former chamber lodges the ganglia of the trigeminal and facial nerves and the latter the head vein and the orbital artery as well as the ventral portion of the large trigeminal ganglion. Ossification of the otic bones has well progressed in the auditory capsule at this stage. As such, in the areas of ossification, which occurs in the dorso-posterior and lateral wall of the auditory capsule, apparent vacuities are created due to the absorption of the underlying cartilages bordered by the ossifying lamellae of the bones. Two such prominent vacuities, one in the lateral wall of the anterior semicircular canal and the other further back in the lateral wall of the lateral semicircular canal are prominent and represent the scene of ossification of the anterior sphenotic and the posterior pteryotic bones respectively. Similarly a large vacuity-like space on the dorso-posterior region of the auditory capsule is created by the ossifying sphenotic bone. The tectum synoticum now forms a very extensive roof to the brain cavity in the auditory region and gives off a small backwardly directed process from its posterior margin which projects over dorsally in between the two occipital arches.

Anteriorly, the ethmoid region is much better developed now and the various cartilages have increased in thickness. The inter-nasal septum forms a thick plate-like cartilage on the dorsal surface of the ethmoid plate and is especially prominent towards its posterior region. Both the orbital cartilage as well as the lamina orbitonasalis now extend
slightly forwards, the former beyond the anterior margin of the sphenoseptal commissure and the latter beyond its fusion with the sphenethmoid commissure. These extensions provide a dorso-lateral roof and lateral wall to hinder region of the olfactory fossa. Thus posteriorly the olfactory fossa gets more or less completely enclosed, laterally by the thick vertical pillar-like lamina orbito-nasalis, ventrally by the lateral extension of the ethmoid plate and dorsally by the sphenoseptal commissure, into which the anterior portion of the cavum orbitonasale opens by the foramen olfactorium advehens. Both the cavum orbitonasales are separated from each other by the posterior extension of the internasal septum. The rostral cartilage has further increased in size and now extends well backwards over the anterior region of the ethmoid plate.

The absorption of the cartilage, already started in the posterior trabecular portion has extended forwards and the paired trabeculae as well as an appreciable portion of the posterior part of the trabecula communis has undergone complete absorption. As a result, the reduced trabecula communis now projects freely backwards from the posterior margin of the ethmoid plate and does not extend beyond the level of the anterior margin of the epiphysial cartilage. Posteriorly, a little distance in front of the place of approximation of the floor of the brain cavity with the floor of the neurocranium, the rudiment of the cartilaginous inter-orbital septum marked out in the preceding stage, now separates off as an independent piece of cartilage due to the absorption of intervening cartilage and takes the
form of a vertical cartilaginous plate in the posterior region between the two eyes. The epiphysial bar now extends backwards and assumes the shape of a triangular cartilaginous piece with the apex directed backwards; the pointed apex represents the developing taenia tecti medialis. The portion of the orbital cartilage in front of the epiphysial cartilage upto the ethmoid region is now reduced to an extremely thin rod of cartilage; (due to partial absorption) whereas its posterior portion stretching between the epiphysial cartilage and the auditory capsule becomes greatly thickened and forms a thick and dorso-ventrally flattened plate-like structure.

The splanchnocranium shows further absorption of the already existing cartilages as well as further ossification. In the mandibular arch, the anterior portion of the pterygoid bar, beyond its articulation with the ethmoid plate, elongates further and reaches slightly beyond the anterior limit of the nasal organ. In the lower jaw, ossification and formation of the dentary bones, started at 8 mm. length of the embryo, has made further progress and approximately about 1/3 of the anterior portion of the Heckel's cartilage, has been replaced by the developing dentary bone; posteriorly, however, the Heckel's cartilage with its coronoid process remains well. In the hyoid arch, the posterior blade-like expansion of the cerato-hyal has further increased in size. In the hyomandibular cartilage, ossification has already progressed well in the region of the foramen for the exit of the hyomandibular branch of the facial nerve due to the absorption of the cartilage all around
the foramen with the result that the hyomandibular nerve now actually passes through a foramen enclosed by bony tissue. The median basihyal also shows extension further forwards. In the branchial arch skeleton the first pharyngobranchial has increased in size and now forms a small rod-like cartilage, instead of the small nodule-like cartilage seen in the previous stage. The second pharyngobranchial has grown further in size, with the two small round pieces of cartilage still attached to its posterior margin. The last pharyngobranchial gets reduced further due to further absorption of the cartilage. All the epibranchials are very well developed, but the third epibranchial continues to be the smallest. The distal portion of the second epibranchial becomes expanded and develops a shallow concavity showing a tendency towards bifurcation following the first one. The fourth epibranchial also expands towards its distal portion forming a blade-like structure. Due to increased absorption and simultaneous ossification, the last cerato-branchial now appears as a bony rod except for a short anterior terminal portion, which remains cartilaginous and a very small nodule-like cartilage towards its extreme hinder end. Ossification is also seen at this stage towards the middle of the fourth pair of ceratobranchials. The median anterior and posterior copulae have increased in size considerably and the anterior one shows two well-developed constrictions between the first and second and second and third pair of hypobranchials. The terminal extremities of the basi-hyal and of the first and second copulae continue to slightly overlap each other at the points of their contact.
STAGE 13. (15.4 mm. length) Plates 69 to 87. Figs. 134 to 167.

1. The Chondrocranium:

(a) Synopsis:

The prootic bridge now becomes very extensive with the conspicuously developed posterior myodome below it. At this stage, the anterior parachordal processes are completely absorbed. The last or the sub-cranial section of the posterior myodome is now provided with a well developed floor formed by the forward lamellar extensions of the developing basi-occipital bone.

In the ethmoid region, the cavum orbitonasale becomes more developed and its anterior portion presents the appearance of a tunnel-like passage. The broad sphenos-epithelial commissure now extends very far backwards, forming a cartilaginous roof over the anterior portion of the orbit. A pair of small independent bones now appears laterally above the anterior region of the ethmoid plate; they seem to correspond to the pre-ethmoid bone as reported in *Esox* by Swinnerton (1902). The trabecula communis gets further reduced in length due to the absorption of cartilage posteriorly. The taenia tecti-medialis now extends further back than in the preceding stage. The orbital cartilage anteriorly between the epipophyseal cartilage and the ethmoid region becomes very slender due to further absorption of the cartilage.

In the splanchnocranium, ossification is now noticeable in the middle portion of all the ceratobranchial.
Detailed Account:

At this stage, the lateral margins of the extensive prootic bridge are continued into the parachordals at the more dorsal general level of the basal plate, leaving the ventrally depressed medial edges of the parachordals free, which extend downwards and inwards underneath the prootic bridge to enclose the sides of the posterior myodome. Posteriorly, however, the prootic bridge as well as the adjacent portions of the basal plate connected to its lateral edges, are much thicker than anteriorly and the whole structure in this region assumes the shape of a semicircular arch like structure. Correspondingly, the myodomic space in this region assumes the shape of a deep inverted gutter-like channel. Anteriorly the prootic bridge is in the form of a flat transverse shelf of cartilage and together with the medially depressed edge of the parachordals offer a somewhat transversely elongated rectangular myodomic space lodging the external rectii muscles. The myodomic space at this stage is enclosed from below by the developing parasphenoid bone. This space is also partitioned into a dorsal and a ventral compartment by a horizontal membranous wall and the dorsal compartment is further divided into two for enclosing the two external rectii muscles. The internal rectii eye muscles, on the other hand, lie in the ventral compartments of the myodomic space which is also divided into two compartments by a vertical partition which is a posterior continuation of the interorbital septum.

The anterior parachordal processes are now completely absorbed and no trace of it is discernible at this stage. The
The notochord has receded further back and is now confined only to the hinder portions of the basal plate. Its anterior tip now projects forwards for a short length into the posterior part of the posterior myodome. Posteriorly the epichordal commissure bridging the hinder portions of the parachordals has grown further in width.

In the auditory region, the posterior vacuity on the floor of the auditory capsule loging the saccular extension of the membranous labyrinth increases in size with the further absorption of the cartilage in that area. Posteriorly the ossification of the ex-occipital bone, already begun in the earlier stage, has made good progress and extends not only into the anterior portions of the occipital arches, but also towards the floor of the hinder part of the auditory capsule bordering the fissura metotica externally. As a result of this extensive ossification, resorption of the cartilages occur in the adjacent areas of the neurocranium fringing the fissura metotica, creating an apparent vacuity all around. Thus the fissura metotica, confluent with the surrounding vacuity, now appears to be a large fossa with no clear outline due to the irregular ossification of the adjacent areas. The tectum synoticum forms a more extensive roof to the chondrocranium and its posterior process becomes developed into a triangular plate of cartilage with its apex directed backwards.

The ethmoid region, attains its maximum development at this stage. The sphenoseptal commissures fused with the massive internasal septum, provide a roof over the posterior
region of the nasal capsule. Posteriorly, the sphenoseptal commissures extend very far backwards, beyond the level of the lamina orbitonasalis, forming cartilaginous roofs over the anterior region of the orbits. However, this apparent portion of the orbit roofed over by the posterior extension of the sphenoseptal commissure really represents portion of the extra-cranial cavum orbitonasale, developed for the transit of the olfactory nerve from the brain cavity to the anteriorly located nasal capsules. The cavum orbitonasales communicate with the corresponding orbital cavity through a wide opening - the fissura orbitonasalis or the orbital foramen - through which the orbitonasal vein and the orbitonasal artery also pass forward. The oblique eye-muscles are attached to the posterior portion of the median septum separating the two cavum orbitonasales, on either side, the attachment of the superior oblique muscle being slightly anterior to that of the inferior oblique muscle. The anterior portion of the cavum orbitonasale, in the region of the lamina orbitonasalis, is bounded by cartilage on all sides, ventrally by the ethmoid plate, medially by the internasal septum, dorsally by the sphenoseptal commissure and laterally by the lamina orbitonasalis. The whole configuration of the cartilages in this part is such that the cavum orbitonasales ending blindly in front have the appearance of a pair of tunnel-like passages hollowed out in the thickness of the hinder portion of the broad internasal septum, and separated from one another by the intervening narrow, vertical portion of the internasal septum. Each cavum orbitonasale opens laterally by the foramen olfactorium advehens into the posterior portion of the nasal
capsule. This foramen is therefore bordered posteriorly by the lamina orbitonasalis, ventrally by the lateral prolongation of the ethmoid plate, dorsally by the sphenoseptal commissure and antero-medially by the internasal septum. In *Tilapia* there is the formation of a pair of a cartilage bones in the pre-ethmoid corner of the ethmoid plate. This was already indicated in the preceding stage and corresponds, in all probability, to the pre-ethmoid bone of Swinnerton (1902) reported in the *Esox* T 2227.

The rostral cartilage has grown further in size and anteriorly its dorsal surface presents a trough-like concavity. The rostrum now extends forwards as far as the posterior portion of the developing pre-maxillary bones and lies ventral to them. Ossification has already started in the posterior portion of the rostral cartilage from its ventral side, invading its cartilage cells.

In the orbito-temporal region, the reduced trabecula communis now projects backwards as a feathery cartilaginous extension from the posterior border of the ethmoid plate. In the posterior portion of the orbits, the cartilaginous inter-orbital septum now attains more or less its maximum development; it now extends forwards up to a point slightly behind the optic nerves (where the two internal rectii muscles just converge and proceed backwards.). From this point, backwards, it increases in height and its middle portion touches the floor of the brain cavity, forming a complete cartilaginous septum between the two orbits. Posteriorly the height of the cartilaginous portion of the internasal septum again decreases gradually. The lower edge of the septum, especially in the
posterior region is bifurcated, the two forks being attached to the two sides of the median ridge of the parasphenoid bone beneath. In the anterior and posterior regions of the cartilaginous interorbital septum, the gap between it and the floor of the brain cavity is completed up by membranous portions of the inter-orbital septum to complete the partition between the orbits, in these regions. Beyond the posterior part of the cartilaginous septum, the membranous interorbital septum continues backwards and serves to separate the two ventral compartments of the posterior myodome from each another. The taeni tecti medialis of the epiphysial cartilage is much better developed now, and extends further backwards than in the preceding stage. It is a more or less triangular, dorsoventrally compressed plate of cartilage attached by its broad base to the posterior margin of the middle portion of the epiphysial cartilage. It runs obliquely backwards and upwards so that its hinder portion is at a higher level than the front portion.

In the mandibular arch, the anterior portion of the pterygoid section extends now further forwards towards the snout beyond its articulation with the ethmoid plate reaching up to the anterior limit of the rostral cartilage. Throughout its length, the pterygoid bar now shows a tendency for perichondral ossification, which is more pronounced in its posterior portion towards the quadrate. Ossification now starts in the articular process of the quadrate and also extends to its adjacent areas. Ossification and absorption of cartilage has also started in the posterior terminal portion of the metapterygoid process of the quadrate, rather irregularly, with
the result that its hindmost cartilaginous portion presents now an irregular outline. Thus it is now difficult to identify the small otic process, which becomes a part of the metapterygoid portion in the ossifying area. The anterior bony portion of the lower jaw extends beyond the level of the pterygoid bar and meet in its fellow of the opposite side in the mid-ventral line. In the hyoid arch, the anterior portion of the hyomandibular base fits into a well marked cup-shaped depression on the ventral surface of the auditory capsule, the depression getting shallower towards the posterior portion of the cartilage until at last only a plane surface of contact is all that is left for the articulation of the hindmost part of the base of the hyomandibular cartilage. As a result of the ossification and complete absorption of the hyosymplectic cartilage, where the foramen for the exit of the hyomandibular branch of the facialis nerve exists, the nerve now passes through the breach created between the hyomandibular and the lower symplectic portion of the hyosymplectic cartilage. As for the branchial arches, first and second pharyngobranchials have increased in size still further. The last pharyngobranchial representing the fused third and fourth pharyngobranchials is reduced further, due to continued absorption of cartilage. Following the first one, the second epibranchial also bifurcates at their distal margin by developing the shallow concavity at their distal margin. Due to the absorption of the intervening cartilage, the basal portion of the fourth epibranchial gets completely detached from its expanded blade-like distal portion now; due to further absorption of the cartilage in the dorsal portion, the latter
now appears as two separate pieces of cartilage situated close to the fused pharyngobranchial of the third and fourth branchial arches. Ossification has already started in all the ceratobranchials in their middle portions with decreasing intensity from the posterior to the anterior ones with the result that in these regions, the original cartilage is gradually absorbed. The ventrally directed process of the third hypobranchial becomes much more prominent than in the previous stage and extends downwards to enclose the ventral aorta from the sides. The basihyal and the first and second copulae do not show any features of interest except that they have further increased in size.