MORPHOLOGY OF THE CHONDROCRANIUM IN THE EMBRYO OF

16 mm. LENGTH.

Plates - 60 to 73. Figs. 88 to 110.

I. The chondrocranium.

The neurocranium is divided into a large posterior portion which is limited anteriorly by the epiphysial bar and a much smaller anterior region. These two portions are separated off from one another by a wide gap in the orbital region.

(a) Basal plate and notochord.

The base of the neurocranium is fully chondrified except for the presence of a pair of small basicapsular fenestrae situated between the parachordals and the auditory capsules at the level of the anterior end of the notochord. The notochord is restricted to the posterior half of the basal plate and the parachordals are united with it on either side. In front of the notochord, the two parachordals have fused with one another to form the prootic bridge which forms the anterior half of the basal plate. Laterally, the parachordals are fused with the ventral wall of the corresponding auditory capsules. Beyond the latter, the parachordals are produced forward into a pair of parachordal processes which are separated off from one another by a narrow elongated gap. Near the anterior region of the
auditory capsule, the floor of the neurocranium is pierced on either side by a large vacuity known as the facial foramen through which the head vein and the hyomandibularis branch of the facial nerve pass out to run ventrally to the neurocranium. The facial foramen is bounded mesially by the parachordal process and antero-laterally by the lateral commissure. Its lateral and hinder limits are formed by the wall of the auditory capsules.

(b) Occipital region.

The hinder ends of the parachordal processes are drawn out into a pair of occipital arches which curve over and fuse with one another dorsally to form a narrow tectum posterius. Laterally, they are connected with the wall of the auditory capsule by their dorso-lateral border only, so that a gap is left between the wall of the auditory capsule and the neural arch forming a foramen metoticum through which the glossopharyngeal and vagus nerves pass obliquely downwards and backwards. The anterior margin of the tectum posterius is fused with the hinder border of the tectum synoticum and the two are not separated off from one another by a gap as in the case of some fishes like Acipenser and Syngnathus.

(c) Auditory region.

The auditory capsule is devoid of a mesial wall but is otherwise fully chondrified. Ventrally, it is
indistinguishably fused with the lateral edge of the corresponding parachordal. The roof of the auditory capsule ends mesially with a free edge except in the hinder region where it is connected with the fellow of the opposite side by a broad tectum synoticum which forms the roof of the cranial cavity. Internally, the cavity of the auditory capsule is crossed by cartilaginous septa of the three semicircular canals. Anteriorly, the auditory capsule is produced into a slender post-orbital process which is fused with the orbital cartilage in front.

(d) **Orbito-temporal region.**

The floor of the orbito-temporal region is practically membranous except for a small, median, triangular piece representing the remnant of the trabecula communis. This piece of cartilage is attached to the hinder end of the anterior portion of the neurocranium. Near the middle of the orbito-temporal region, immediately behind the optic chiasma, the floor shows another small median piece of cartilage, the basi-sphenoid cartilage, which is not connected with any other cartilaginous element of the neurocranium. It lies immediately dorsal to the developing parasphenoid bone. The posterior limit of the orbito-temporal region is represented by the cartilaginous lateral commissure which joins the anterior end of the parachordal process with the auditory capsule. The lateral commissure runs obliquely backwards from the parachordal process and
forms the lateral wall of the large trigemino-facialis chamber which lodges the Gasserian and Geniculate ganglia of the trigeminal and facial nerves. This chamber opens widely in front into the orbit and through this opening the head vein, the secondary afferent pseudobranchial artery and the branches of the trigeminal nerve pass out. Below the base of the brain cavity, the two orbital cavities are separated off from one another by a median, vertical, membranous interorbital septum which is attached along its dorsal edge to the ventral membranous wall of the brain cavity. Ventrally, the interorbital septum extends from the trabecular communis in front to the parasphenoid behind.

The lateral wall of the orbito-temporal region is membranous except for the orbital cartilage which runs along its dorso-lateral region. The orbital cartilage is present only in the hinder part of the orbital region and extends from the epiphysial cartilage to the post-orbital process of the auditory capsule with which it is fused. Anteriorly, the orbital bar is absent but its anteriormost tip is recognisable as a small backwardly directed process from the hinder side of the ethmoid region.

The orbito-temporal region is partly roofed over by an epiphysial cartilage but is otherwise membranous. The epiphysial cartilage runs across the middle of this region as a transverse bar of cartilage which is prolonged backward along the mid-dorsal line as the taenia tecti medialis. The
latter is in the form of a triangular plate-like cartilage of which the broad base is continuous with the epiphysial cartilage and the apex directed backwards.

(e) Ethmoid region.

The ethmoid plate forms the floor of the ethmoid region and this is continued behind as a triangular trabecula communis with the apex directed backwards. The trabecula communis is greatly reduced and its posterior apex does not project behind beyond the anterior remnant of the orbital cartilage. The ethmoid plate is in the form of a thickened plate-like cartilage and is produced postero-laterally into a pair of small lateral processes. Anteriorly, the remnant of the orbital cartilage divides into two processes, a posterior sphenethmoid process and an anterior sphenoseptal process. The sphenethmoid process is a very small one and soon fuses with the lamina orbitonasalis. The latter is in the form of a small vertical cartilaginous rod which runs ventrally to fuse with the lateral process of the ethmoid plate. The sphenoseptal processes are much larger in size and dorsally they fuse with one another to form a large plate-like sphenoseptal commissure. In the posterior region, the sphenoseptal commissure extends very far backward even beyond the level of the lamina orbitonasalis, forming a cartilaginous roof over the anterior region of the orbit and the posterior ethmoid region. Anteriorly, the sphenoseptal commissure is fused with the dorsal surface of a thick cartilaginous nasal septum which arises upwards from
the ethmoid plate along its mid-dorsal line. In Belone, the foramen through which the olfactory nerve comes out from the cranial wall proper, opens into an extra-cranial space known as the cavum orbitonasale. Ventrally, the cavum orbitonasale is enclosed by the ethmoid plate and dorsally by the sphenoseptal commissure; the left and right cavum orbitonasales are separated off from one another by a vertical membranous partition formed by the posterior part of the nasal septum. Each cavum orbitonasale opens laterally by a wide mouthed foramen olfactorium advehens into the nasal capsule. This foramen is bounded posteriorly by the lamina orbitonasalis, ventrally by the lateral projection of the ethmoid plate and dorsally by the lateral prolongation of the sphenoseptal commissure (which is continued laterally to form the dorsal wall of the nasal capsule) and anteriorly by the nasal septum. Anteriorly, the cavum orbitonasales of the two sides end blindly in the form of a pair of small cavities hollowed out in the hinder wall of the nasal septum and are separated off from one another by a small, narrow cartilaginous nasal septum. The oblique muscles of the eye are inserted in these posterior cavities or hollows of the nasal septum throughout its length. The nasal septum is fused with the ethmoid plate and is in the form of a broad, thick plate-like cartilage which extends forward and is hollowed out on either side to form the median wall of the nasal fossae. Beyond the latter, the fused ethmoid plate and the nasal septum is continued forward as the rostrum. Immediately beyond the
anterior end of the rostrum, there is a small median piece of cartilage which is situated in between the base of the developing premaxillary bones and represents the premaxillary cartilage.

The nasal capsules are very incompletely chondrified and each is in the form of a shallow pit-like structure which is widely open on the sides and in front. The hinder wall of the nasal capsule is formed by the lamina orbitonasalis, the ventral by the lateral portion of the ethmoid plate and the mesial wall by the nasal septum. The dorsal wall is, however, practically non-existent and is represented in the hinder region by slight lateral expansions of the dorso-lateral edge of the sphenoseptal commissure.

(f) Visceral arches.

As usual, the visceral arches are represented by the mandibular arch, the hyoid arch, and the five pairs of branchial arches.

The mandibular arch is represented by paired pterygo-quadrate bars in the upper jaw and paired Meckel’s cartilages in the lower jaw. The pterygoquadrate bar can be divided into a posterior quadrate and an anterior pterygoid portion, though there is no line of demarcation between the two. The quadrate portion is in the form of a slender elongated bar of cartilage which for the greater part of its length rests on the hyosymplectic cartilage of
the hyoid arch. The pterygoid portion arises from the distal end of the quadrate immediately before it gives articulation to the Meckel's cartilage. The pterygoid portion of the pterygoquadrate runs obliquely upwards and forwards towards the ethmoid region; its middle portion is comparatively slender but distally it expands to form a laterally compressed plate-like portion which articulates posteriorly with the lamina orbitonasalis by an ethmopalatine process and anteriorly with the ethmoid by a rostropalatine process. The Meckel's cartilage is in the form of a well developed, elongated, rod-like cartilaginous bar which articulates posteriorly with the distal end of the quadrate; anteriorly, it extends much forward than the pterygoquadrate as at this stage, the lower jaw of the embryo is longer than its upper jaw. Anteriorly, the two Meckel's cartilages are encased in developing bone and through their anterior ends come close together, there is no fusion between them.

On each side, the hyoid arch is represented by hyosymplectic, interhyal (stylohyal), ceratohyal, and hypohyal cartilages. The hyosymplectic cartilage is divisible into a proximal hyomandibular and a distal symplectic portion. The hyomandibular portion of the hyosymplectic is represented by a broad triangular cartilage which is attached by its broad base to the ventral wall of the auditory capsule and its apex is prolonged forward into the symplectic portion. The hyomandibular portion is pierced by a small foramen for
the passage of the hyomandibularis branch of the facial nerve. The symplectic portion is in the form of a slender elongated cartilaginous rod which underlies the quadrate; anteriorly, it stops short just behind the anterior end of the quadrate portion of the pterygoquadrate. The internyal cartilage is a small and rounded cartilage and lies between the postero-dorsal region of the ceratohyal and the ventral surface of the symplectic portion of the hyosymplectic. The ceratohyal is in the form of a broad elongated cartilage and runs forward obliquely towards the median line where it is fused with a small hypohyal cartilage. The hypohyals of the two sides meet each other along the mid-ventral line. The basihyal is situated along the median line and is in the form of an elongated, triangular, plate-like cartilage with its broad base directed forward and the apex backward between the two hypohyals. The basihyal cartilage forms the anteriormost element of the median copula.

In the branchial arches, the pharyngobranchials are represented by a small pharyngobranchial representing the first branchial arch and an elongated one representing the fused pharyngobranchial elements of the second, third, and fourth branchial arches. The latter is in the form of an elongated rod-like cartilage which runs dorsally to the third and fourth branchial arches but its hindermost portion turns ventral to the fourth epibranchial cartilage. Each epibranchial is in the form of a small cartilage
situated dorsally to the hinder region of the corresponding ceratobranchial cartilage. The first and second epibranchials are connected with the corresponding ceratobranchial cartilage, but the third and fourth epibranchials are free. All the five pairs of ceratobranchial cartilages are in the form of narrow, elongated cartilaginous rods and extend forward and inward towards the median copula. The first four ceratobranchials are free from one another and progressively decrease in length from first to fourth. The ceratobranchials of the fifth branchial arch are fused with one another to form a median inverted Y-shaped piece of cartilage; the median limb lies behind the copula and is much longer than the two posteriorly directed limbs. The hypobranchial elements are present only in the first three branchial arches. In the first and second arches, they are fused with the corresponding ceratobranchials on the one hand and meet the copula on the other. The hypobranchial of the third branchial arch is joined with the corresponding ceratobranchial element, but is separated off from the copula by a narrow gap.

The copula is in the form of an elongated median cartilaginous rod which is fused anteriorly with the hinder end of the basihyal cartilage. Posteriorly, the copula stops short just in front of the anterior tip of the fourth pair of ceratobranchial cartilages. The copula is not uniformly thick throughout its length but is constricted
between the basihyal and the first pair of hypobranchials and between the first and second pair of hypobranchial cartilages. Behind the second pair of hypobranchials, the copula extends backward as a slender rod-like structure.

II. Eye muscles.

The inferior oblique muscle arises from the anterior blind end of the cavum orbitonasalis in the region of the internasal septum; anteriorly, it arises partly from the floor of the sphenoseptal commissure and the cartilaginous internasal septum and partly from the anterior membranous portion of the interorbital septum which lies immediately behind the cartilaginous internasal septum. It runs obliquely backwards and outwards and running dorso-laterally to the trabecula communis, passes into the orbit to become inserted on the antero-ventral region of the eyeball.

The superior oblique muscle arises from the anterio-most portion of the interorbital septum immediately behind the cartilaginous internasal septum. The superior oblique muscles of the two sides run straight back through the cavum orbitonasales just below the sphenoseptal commissure and just beyond the level of the insertion of the inferior oblique muscle on the eyeball, turn obliquely outwards to get inserted on the dorsal region of the eyeball.

The anterior, superior, and inferior rectii muscles
arise close together from the dura mater along the ventrolateral region of the mid-brain. The anterior rectus muscle arises internally to the inferior rectus muscle and runs forward and upward in the orbit. During its course, it passes ventrally to the optic nerve and externally to the basisphenoid cartilage; further forward, it runs externally to the parasphenoid bone and finally gets inserted along the mesial surface of the eyeball somewhat beyond the level of the insertion of the superior oblique muscle. The superior rectus muscle arises immediately above the inferior rectus muscle and runs upwards along the dura mater to get inserted on the dorsal region of the eyeball. In the region of the optic nerve, it passes dorsal to the nerve. The inferior rectus muscle arises from the dura mater from a place which lies just behind the origin of the anterior rectus muscle and runs obliquely forwards and outwards in the orbit. During its course, it runs ventral to the optic nerve and external to the anterior rectus and is finally inserted on the ventral region of the eyeball. The posterior rectus muscle arises from the dura mater close to the mid-ventral line and runs obliquely outwards and forwards. During its course, it passes dorsally to the anteriormost end of the parachordal process and finally gets inserted on the hinder region of the eyeball.
III. Cranial nerves.

The olfactory nerve arises from the ventral region of the olfactory lobe and runs forward in the orbit below the sphenoseptal commissure. Further forward, it runs dorsal to the superior oblique muscle and enters the cavum orbitonasale and finally passes out through the foramen advehens into the olfactory pit to innervate the olfactory organ.

The optic nerves arise from the ventral region of the mid-brain and, after coming out of the membranous wall of the brain cavity, cross each other above the anterior rectus muscle and run obliquely forward to supply the eyes of the opposite sides. Beyond the crossing of the optic nerves, each optic nerve passes forward between the anterior rectus and inferior rectus muscles and finally enters the eye immediately in front of the insertion of the latter muscle.

The oculomotor nerve arises from the ventro-lateral region of the brain and, after coming out of the membranous wall of the brain cavity, runs dorsally to the posterior rectus muscle to divide into two branches. One of these branches runs forward and upward between the eye and the lateral wall of the brain to innervate the posterior rectus muscle while the other branch turns downward to divide into three branches to innervate the inferior oblique, anterior
rectus and inferior rectus muscles. The branches supplying the anterior rectus and inferior rectus muscles run dorsal to the latter muscle. The branch which supplies the inferior oblique muscle, however, passes forward dorsal to the inferior rectus muscle and ventral to the anterior rectus muscle close to the interorbital septum; further forward, it runs dorsal to the trabecula communis and turns outwards to supply the inferior oblique muscle as the latter passes to the eyeball.

The trochlear nerve arises from the mid-brain close to the origin of the oculomotor nerve. It runs forward close to the membranous wall of the brain cavity and passing dorsal to the superior rectus muscle finally innervates the superior oblique muscle of the eye.

The trigeminal nerve arises from the ventro-lateral region of the hind brain behind the origin of the trochlear nerve. After coming out of the membranous wall of the brain cavity, it passes into the trigemino-facialis chamber in which it swells out to form a large Gasserian ganglion. It gives off an ophthalmic and a maxillo-mandibularis branch which pass forward into the orbit through the wide anterior opening of the trigemino-facialis chamber. The maxillo-mandibularis branch of the trigeminal nerve arises from the anterior side of the Gasserian ganglion as a thick nerve. It passes forward below the posterior rectus
muscle and further forward, below the inferior rectus muscle of the eye, it runs externally to the pterygoid portion of the pterygoquadrate bar. In the region, where the Meckel's cartilage articulates with the quadrate, the maxillo-mandibularis branch divides into a maxillaris and a mandibularis nerve. The maxillaris nerve runs obliquely forwards and outwards below the eye and the inferior oblique muscle to the region of the upper jaw. The mandibularis nerve curves downwards and passes forward into the lower jaw running dorso-laterally along the Meckel's cartilage. The ophthalmic branch arises further backwards from the lateral border of the Gasserian ganglion behind the origin of the maxillo-mandibularis branch. It runs forward in the orbit close to the membranous wall of the brain cavity and soon comes to lie below the orbital cartilage. In the region of the epiphsial cartilage, it runs externally to the orbital cartilage and further forward, dorsal to the superior rectus and superior oblique muscles and finally comes to lie over the sphenoseptal commissure. It runs close to the lateral margin of the sphenoseptal commissure sandwiched between the cartilaginous wall of the latter and the developing orbital bone above it. Finally, it passes downwards through a tunnel in the cartilaginous dorsal wall of the olfactory capsule and enters the latter to innervate the anterior region of the head.
The abducens nerve arises from the sides of the medulla oblongata much behind the origin of the trigeminal nerve. For a long distance, it runs forward within the cranial cavity along the ventral side of the medulla oblongata and the lobi inferiores. Finally, it passes to the posterior rectus muscle of the eye where the latter arises from the membranous wall of the brain cavity.

The facial nerve arises from the ventro-lateral region of the hind-brain and almost immediately swells out to form a large facial or Geniculate ganglion which occupies the hinder portion of the trigemino-facialis chamber. In fact, the facial ganglion extends forward upto the hinder region of the Gasserian ganglion where both can be seen occupying the trigemino-facialis chamber, the hinder part of the Gasserian ganglion lying ventral to the anterior part of the facial ganglion. Anteriorly, the facial ganglion gives off an ophthalmic branch which soon unites with the ophthalmic branch of the trigeminal nerve and passes forward along with the latter to the olfactory region. Near its middle, the facial ganglion gives off ventromesially a small pseudobranchial nerve which innervates the pseudobranch and further back it gives off a palatine nerve. The latter, near its origin, is joined by the palatine branch of the glossopharyngeal nerve and thereafter the palatine nerve runs forward in the trigemino-facialis chamber immediately above the lateral commissure;
ultimately it passes downwards behind the place where the lateral commissure joins the parachordal process to innervate the palate.

The auditory nerve arises from the dorso-lateral region of the medulla oblongata and passes downwards between the brain and the internal ear and divides into branches to innervate the sensory areas of the latter.

The glossopharyngeal nerve arises further back from the sides of the medulla oblongata and becomes enlarged to form a jugular ganglion situated within the cranial cavity. Finally, it comes out of the cranial cavity through the foramen metoticum along with the vagus nerve and runs forward closely applied to the ventral surface of the basal plate internally to the head vein. In the region of the basicapsular fenestra, it passes immediately below it. Further forward, in the region of the first branchial arch, it gives off a small palatine branch which runs forward internally to the hyomandibular branch of the facial nerve near its origin to form a Jacobson's anastomosis. Finally, the main branch of the glossopharyngeal nerve passes downwards to innervate the first branchial arch.

The vagus nerve arises from the dorso-lateral region of the medulla oblongata and passes ventrally downwards between the brain and the internal ear. After coming out of the cranial cavity through the foramen metoticum, the
vagus ganglion lies on the lateral side of the head vein below the auditory capsules. Anteriorly, the vagus ganglion gives rise to a branchialis nerve which soon passes forward along the ventral side of the head vein to innervate the second, third, and fourth branchial arches. Posteriorly, the vagus ganglion gives rise to a lateralis and visceralis nerve. The lateralis nerve runs back along the dorsal side of the head vein to the trunk region. The visceralis nerve runs obliquely backwards and downwards along the ventral side of the head vein to innervate the visceral organs of the trunk.

IV. Main blood vessels of the head region.

(a) Arteries.

Posteriorly, in the region of the occipital arch, the dorsal aorta runs below the notochord and then divides into a pair of lateral aortae or supra-branchial arteries. Immediately behind the region where the glossopharyngeal and the vagus nerves come out of the cranium, the lateral aorta receives the common stalk of the third and fourth efferent branchial arteries. Further forward, the lateral aorta receives the second and first efferent branchial arteries. Beyond the first efferent branchial artery, the lateral aorta is continued forward below the basal plate as the carotid artery. In the region of the facial foramen, the common carotid gives off an orbital artery.
which runs below the head vein and the palatine branch of
the facial nerve and enters the trigemino-facialis chamber.
In the region where the lateral commissure joins the
parachordal cartilage, the orbital artery runs downwards
and backwards and gives off a secondary afferent pseudo-
branchial artery and a small branch to the operculum.
Beyond the origin of the orbital artery, the carotid artery
is continued forward as the internal carotid artery. It
runs forward ventral to the parachordal process and soon
gives off an orbitonasal artery which runs forward ventral
to the anterior rectus muscle and in the region of the
optic chiasma passes internal to the anterior rectus muscle
close to the median line; further forward, the orbitonasal
artery runs dorsal to the anterior rectus muscle and passes
over the retinal artery and the oculomotor nerve. Finally,
the orbitonasal artery runs forward between the superior and
inferior oblique muscles and enters the olfactory capsule
through the foramen advehens. Beyond the origin of the
orbitonasal artery, the internal carotid artery runs forward
close to the median line below the brain case and soon the
arteries of the two sides are connected with one another near
the origin of the anterior, inferior, and superior rectus
eye muscles by a circulus cephalicus. Immediately behind
the latter, the internal carotid artery gives off a small
posterior cerebral artery to the brain. Beyond the circulus
cephalicus, the internal carotid artery of each side is
continued forward and soon gives off an optic artery which runs downwards and forwards along the optic nerve to the eye as its arteria centralis retinae. Beyond this place, the internal carotid artery passes dorsal to the optic nerve and after giving off a small anterior cerebral artery to the brain, runs forwards and downwards ventral to the orbitonasal artery. Further forward, the internal carotid runs across the orbit as the retinal artery to supply the anterior region of the eye.

The blood from the pseudobranch is collected by a large efferent pseudobranchial artery. It runs forward external to the orbitonasal artery and immediately behind the circulus cephalicus curves round the orbitonasal artery to enter the orbit. In the course round the orbitonasal artery, it passes very close to the internal carotid artery but there is no connection between the two arteries. Further forward, it runs across the orbit as the ophthalmica magna artery to supply the choroid gland of the eye. During its course, the ophthalmica magna artery passes ventral to the oculomotor nerve and superior rectus muscle but dorsal to the inferior rectus muscle; further forward, during its course towards the eyeball, it runs dorsal to the optic nerve and optic artery.

(b) Veins.

An orbitonasal vein arises from each olfactory sac
and runs backwards through the foramen advehens into the cavum orbitonasale. It runs backwards immediately below the sphenoseptal commissure but dorsal to the olfactory nerve and superior oblique muscle. Further back, the orbitonasal vein runs along the olfactory lobe and passes dorsal to the trochlear nerve. At the place where the epiphysial cartilage gets separated from the orbital cartilage, the orbitonasal vein receives a small anterior cerebral vein from the brain. The orbitonasal vein finally joins the superior orbital sinus coming from the posterior dorsal surface of the eye. The main vein of the orbit is represented by a large inferior orbital sinus which arises from the ventral surface of the eye immediately behind and dorsal to the optic artery but ventral to the ophthalmica magna artery. Posteriorly, the inferior orbital sinus turns round the ophthalmica magna artery and passes dorsal to it. It then passes backwards running ventral to the oculomotor nerve and, during its course, receives a large pituitary vein from the hypophysis. It then passes backwards over the posterior rectus muscle and is joined by the superior orbital sinus to form the head vein. The latter passes backwards through the trigemino-facialis chamber internal to the ganglionic mass and receives a mandibular vein on its ventral side and soon after, a posterior cerebral vein on its dorsal surface from the brain. The head vein then passes backwards running between the
facial ganglion and the palatine branch of the facial nerve and passing ventral to the facial ganglion comes out through the facial foramen. It now lies internal to the hyomandibular muscle but external to the hyomandibularis branch of the facial nerve. A large vein from the hyoid arch now joins the head vein in the region where the hyomandibularis branch of the facial nerve is given from the facial ganglion. Further back, the head vein runs below the auditory capsule and, as the head vein passes internal to the hyomandibular muscle, it represents the secondary vein. Finally, the head vein passes backwards internal to the glossopharyngeal and the vagus nerve.