

# THE DEVELOPMENT OF THE CHONDROCRANIUM IN *TRICHOPODUS TRICHOPTERUS* (Pall.)

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## INTRODUCTION

VERY little work has been done on the development of fish skulls in India. In view of this, the present investigation was undertaken in order to examine the development of the chondrocranium in a fresh-water fish—*Trichopodus trichopterus* (Pall.), belonging to the family Anabantidæ. As the fish breeds easily in the laboratory, it was possible to collect successive stages in development in order to get a closely graded series.

## MATERIAL AND METHODS

The fish bred on Saturday, the 24th January 1954, and the female was removed immediately after. The eggs hatched the next day at about 4–30 p.m. and the first batch of embryos was fixed 20 hours after hatching. The successive stages were fixed at frequent intervals to give a closely graded range. Out of 80 stages fixed only 10 stages have been described in this paper.

The larval stages were fixed in piciformol and acetic-alcohol. The serial sections of various stages were cut at 10 micra and stained mainly with Delafield's hæmatoxylin. No counterstain was used. The stages in which the bones had already developed, were decalcified in a solution of

one part of concentrated nitric acid in hundred parts of 70 per cent alcohol. Bulk stained preparations were made by van Wijhe's (1902) technique for the study of the development of the chondrocranium. Methylene blue gave better results than Victoria or Toluidin blue.

Wax model reconstructions were prepared in several cases from series of transverse sections. Graphic reconstructions were also made for studying the chondrocranium.

#### OBSERVATIONS

*Stage 1* ( $37\frac{1}{2}$  hours after hatching. Total length 2.4 mm.) (Fig. 1).—The trabecular rudiments (Fig. 1, *tc*) are appearing as independent rod-like procartilages, placed ventrally in the orbito-temporal region.

The notochord (*n*) is distinctly seen. On either side of the notochord are noticed plate-like procartilaginous parachordals (Fig. 1, *pc*). They are not so distinct as the trabeculæ. The auditory sacs are formed but the capsular cartilages are not laid down and concentration of mesenchymatous cells is seen in this region.

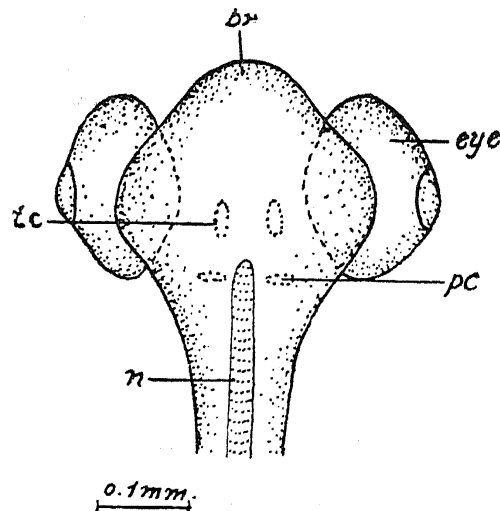


FIG. 1. Dorsal view of the brain and eyes of *Trichopterus trichopterus* (Pall.). Embryo 2.4 mm. long (model), stage 1.

The visceral skeleton is not yet chondrified. Accumulation of mesenchyme cells can be noticed in this region.

*Stage 2* ( $40\frac{1}{2}$  hours after hatching. Total length 2.5 mm.) (Figs. 2 and 3).—The cartilaginous trabeculæ (Fig. 2, *tc*) are better formed at this stage. They unite anteriorly to form a thin ethmoid plate (*ep*) which is about 60 micra in length. Posteriorly the trabeculæ unite with the anterior ends of the parachordals thus enclosing a large hypophysial fenestra (*hf*). The

notochord (*n*) extends anteriorly into the hypophysial fenestra. The parachordals (Fig. 2, *pc*) are broader than the trabeculae and lie on either side of the notochord. The rudiments of the auditory cartilages (*ac*) with well-developed anterior ends have appeared and they form the floor for the auditory vesicles. Each parachordal (*pc*) is united with the auditory cartilage of its side by means of a broad anterior basicapsular commissure (*abc*) and a small posterior basivestibular commissure (*bvc*). A small basicapsular fenestra (*bcf*) is enclosed between these two commissures. The branches of the trigeminal and facial nerves pass in front of the anterior basicapsular commissure. No side wall or cartilaginous roof is formed for the brain in this stage. The rudiments of the occipital arches (*oa*) are noticed on the posterior side of the parachordals.

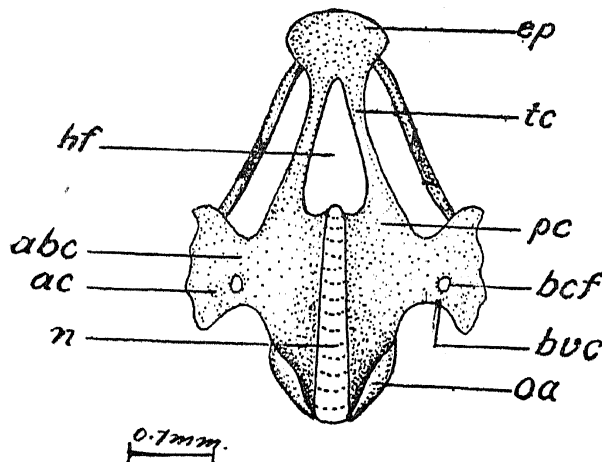


FIG. 2. Dorsal view of the chondrocranium of *T. trichopterus*, stage 2. Total length of larva 2.5 mm. (model). The hypobranchial arches are not shown.

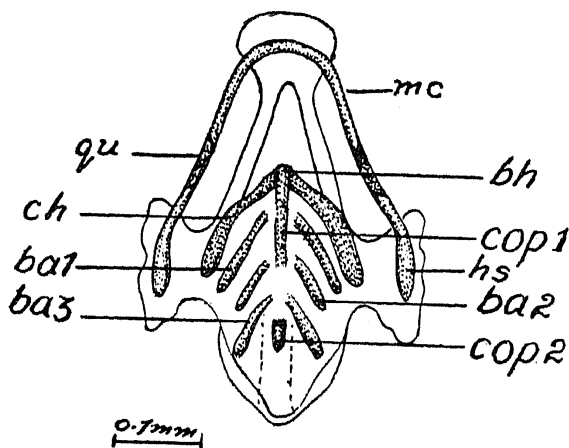


FIG. 3. Ventral view of the visceral arches of stage 8 (model).

The chondrification of some of the visceral arch elements (Fig. 3) has taken place. The two rami of Meckel's cartilage (*mc*) are united anteriorly to form a symphysis.

The pterygoquadrate is represented only by its quadrate portion (Fig. 3, *qu*). Posteriorly the quadrate is in contact with the lower portion of the hyosymplectic cartilage (*hs*). The hyosymplectic articulates with the ventral side of the auditory cartilage and functions as the suspensorium for both the jaws. The basihyal (*bh*) is continuous posteriorly with the basibranchial. It does not extend anteriorly beyond the ceratohyal (*ch*) in this stage. The basibranchials have united to form two copulæ, the anterior or the first copula (*cop 1*) continuous with the basihyal and the posterior one or second copula (*cop 2*), situated behind the first copula with a gap in between. The first copula extends behind up to the second branchial arch in this stage. The first three arches (*ba 1-3*) have appeared in this stage in the form of cartilaginous bars situated on either side of the copula. They are not differentiated into the various branchial elements. The branchial arches ventrally do not reach the copula.

*Stage 3* (50 hours after hatching. Total length 2.8 mm.).—Except that the trabeculæ are more distinctly seen in this stage no new elements are added in the ethmoid region. The parachordals have increased in width. The basicapsular fenestra has also increased in size.

The pterygoquadrate bar has increased in width and extends slightly anteriorly. It is independent of Meckel's cartilage in this stage. The hyoid cornu is well developed and it unites dorsally with the hyosymplectic cartilage through a small procartilaginous stylohyal measuring about 10 micra.

The fourth branchial bar appears in this stage but does not reach the second copula ventrally. The first copula extends up to the third branchial arch. A pharyngobranchial is seen on either side but it is not connected to any of the branchial bars.

*Stage 4* (55 hours after hatching. Total length 3 mm.).—The ethmoid plate has increased in width. The trabeculæ though slightly reduced in thickness are continuous behind with the parachordals.

The occipital arches extend anteriorly but do not reach the auditory region. The rudiments of the auditory capsular roof and side walls are making their appearance.

The stylohyal which was noticed as a small procartilaginous piece in the earlier stage now forms a broad cartilaginous structure, connecting the ceratohyal and the hyosymplectic.

The fifth arch has appeared measuring 40 micra.

*Stage 5* (64 hours after hatching. Total length 3.0 mm.).—There is not much advance in this stage over the previous one excepting for a general

growth in all the cartilages present. The head vein is distinctly seen between the parachordal and the auditory capsule.

*Stage 6* (69 hours after hatching. Total length 3.2 mm.).—The ethmoid region extends approximately between 80 and 90 micra. The basivestibular commissure has slightly increased in thickness.

The second copula supporting the fourth branchial arch has slightly increased in length.

*Stage 7* (98½ hours after hatching. Total length 3.5 mm.).—The ethmoid plate has increased in size. The lamina orbitonasalis is not yet chondrified. Part of the dorsal epiphysial cartilage which has just appeared, measures about 10 micra and is one layer in thickness. The orbital cartilage is formed and is continuous with the epiphysial cartilage. It extends about 30 micra in front and 80 micra behind the epiphysial cartilage. The orbital cartilage is broader anteriorly and lies between the ethmoid and auditory regions but does not reach them.

The fifth branchial arch extends posterolaterally for about 100 to 110 micra, and consists of a single piece of cartilage which is anteriorly cylindrical, posteriorly slightly broader and dorsoventrally compressed. The first pharyngobranchial appears for the first time as a small circular piece of cartilage, extending up to 10 micra. It does not unite with the first ceratobranchial. The second and the third pharyngobranchials are distinctly seen to unite with the second and third ceratobranchials respectively. They seem to arise from the pharyngobranchial of the earlier stages.

*Stage 8* (16th day after hatching. Total length 4.0 mm.) (Figs. 4-7).—The ethmoid plate (Figs. 4 and 5, *ep*) is rounded anteriorly as in previous stages. The medial nasal septum (Fig. 4, *ns*) is appearing. The trabeculae have united to form the trabecula communis (*tcom*) thus reducing the extent of the hypophysial fenestra (*hf*). They are continuous posteriorly with the basal plate. The lamina orbitonasalis is noticed in one section. The orbital cartilage is well formed and unites with the auditory capsule by means of the post-orbital process, not seen in the earlier stages. The epiphysial cartilage (*epb*) has taken a definite shape with an anterior bend in the middle. The auditory capsule (*ac*) shows slight advance over the previous stage and its roof is being formed. The trigeminofacialis chamber (Fig. 5, *tfc*) is situated in front of the basicapsular fenestra (*bcf*) and is bounded anteriorly by the lateral commissure (*lc*). The pro-otic and the post-palatine processes forming the lateral commissure cannot be made out as arising independently from different parts of the cranium either in this stage or in the earlier stages examined.

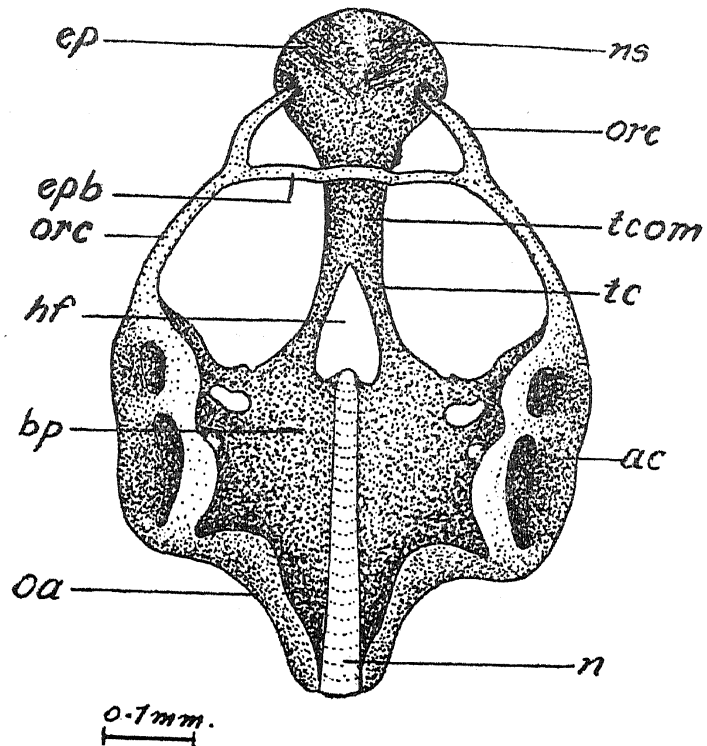


FIG. 4. Dorsal view of the chondrocranium of *T. trichopterus*, stage 8. Total length of larva 4.0 mm. (model). The visceral arches are not shown.

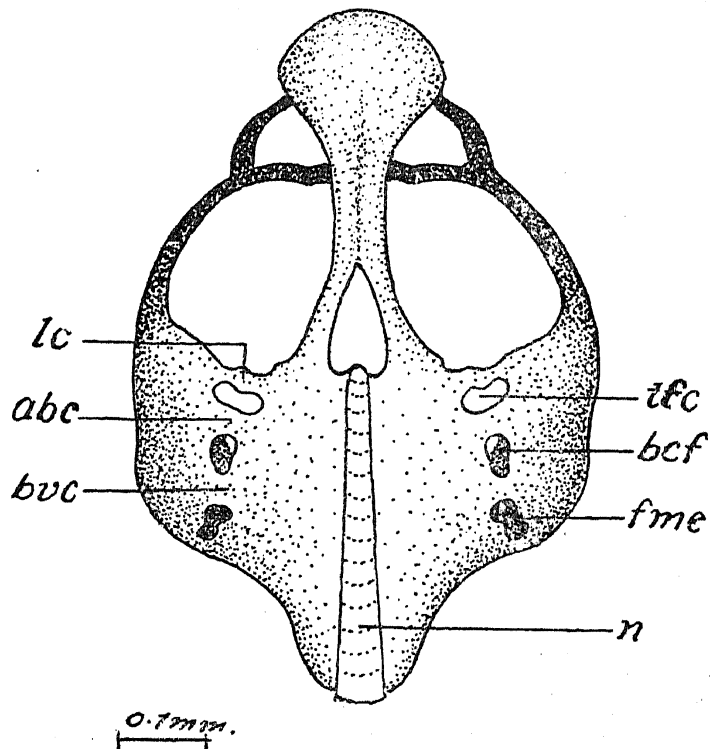


FIG. 5. Ventral view of the chondrocranium of stage 8 (model),

The synotic tectum is not formed in this stage. The occipital arches (Fig. 4, *oa*) are well formed and extend anterolaterally to join the hind end of the auditory capsules. The metotic foramen (Fig. 5, *fme*) is formed through which the IXth and Xth cranial nerves pass to the exterior.

The hyosymplectic cartilage (Fig. 6, *hs*) has increased in size. It bears a small foramen (*fh*) for the hyomandibular branch of the facial nerve. The pterygoid process (*ptp*) of the pterygoquadrate cartilage extends anteriorly up to the ethmoid plate but does not articulate with it in this stage.

The broad and anteriorly rounded basihyal (Fig. 7, *bh*) continues behind into the first copula. The paired hypohyals (*hh*) are well defined and they unite with each other on the ventral side of the basihyal. The first copula after giving attachment to the first three pairs of branchial arches slightly bends ventrally and then extends posteriorly for over 20 micra below the second copula. The second copula (*cop 2*) is small and gives attachment mainly to the fourth and the fifth pairs of branchial arches.

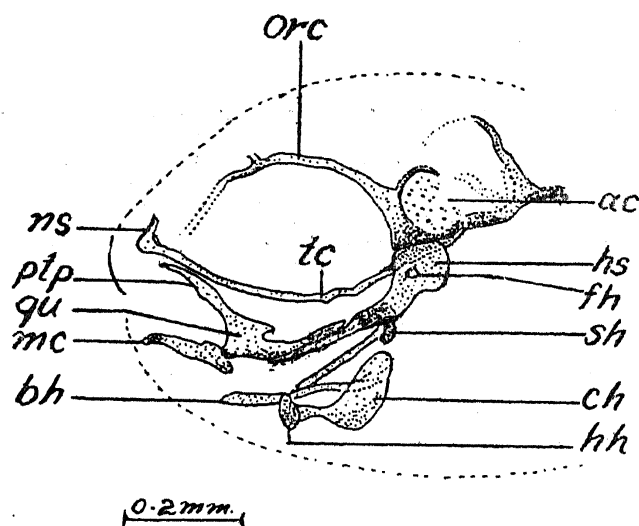


FIG. 6. Lateral view of the chondrocranium of stage 8 (van Wijhe's technique).

The first hypobranchial is distinct from the first ceratobranchial. The demarcation line between the epibranchials and the ceratobranchials cannot be made out at this stage. The last pharyngobranchial (*phb* 3 and 4) appears to be a combined one as it joins the third and fourth branchial arches, formed probably by the third and fourth pharyngobranchials.

**Stage 9** (Total length 6.0 mm.) (Figs. 8-11).—The ethmoid plate (Fig. 8, *ep*) shows two small projections anterolaterally. The median nasal septum (*ns*) which arises in the anterior part of the ethmoid plate is well developed. Dorsolaterally it is united with the sphenoseptal commissure (*sphc*) of the

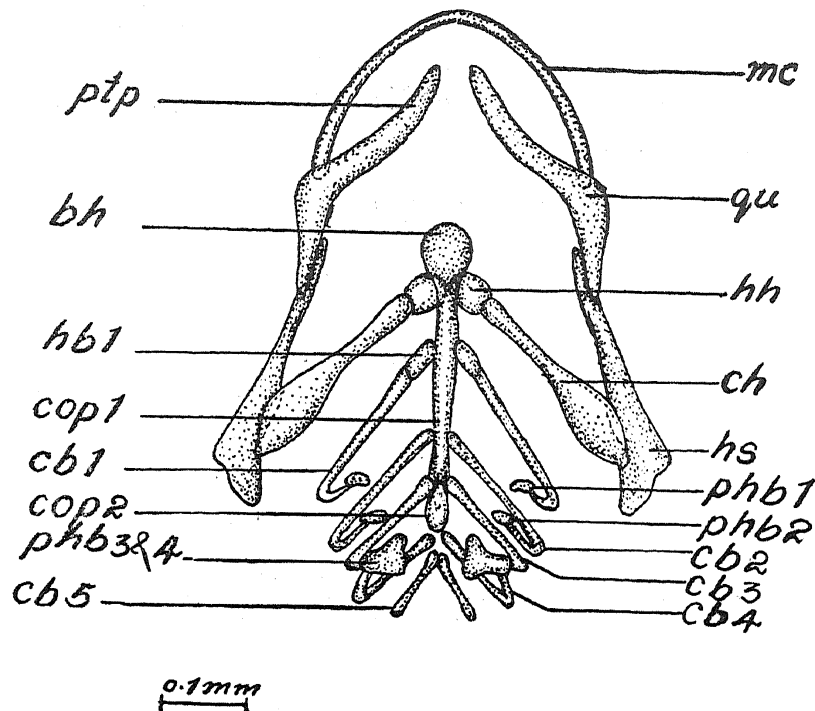


FIG. 7. Ventral view of the visceral arches of *T. trichopterus* of stage 8 (model).

orbital cartilage. The lamina orbitonasalis (Fig. 8, *lon*) is well developed and joins dorsally the orbital cartilage. The trabecula communis (*tcom*) has lost its connection posteriorly with the basal plate so that the hypophysial fenestra becomes obliterated.

The orbital cartilage (Fig. 8, *orc*) is quite prominent and develops the sphenoseptal commissure anteriorly. The epiphysial cartilage (*epb*) is broadened particularly in the middle.

The notochord is squeezed out of the basal plate (Figs. 8 and 9, *bp*) excepting in the posterior region of the cranium. Anteromedially the basal plate has a small notch which marks the posterior limit of the hypophysial fenestra. The auditory capsule is well developed and shows internally two septa—the septum semicircularis lateralis and the septum semicircularis posterius. The roof of the auditory capsule is completed and the synotic tectum (Fig. 8, *tsy*) connecting the two capsules dorsally is well developed. The lateral and the anterior basicapsular commissures are ossified and are no longer cartilaginous. The head vein and the orbital artery become enclosed between the inner and the outer lamellæ of the pro-otic bone, in a space termed pars jugularis of the trigeminofacialis chamber. This chamber is thus separated from the pars ganglionaris (V and VII ganglia) by the inner lamella of the pro-otic bone,



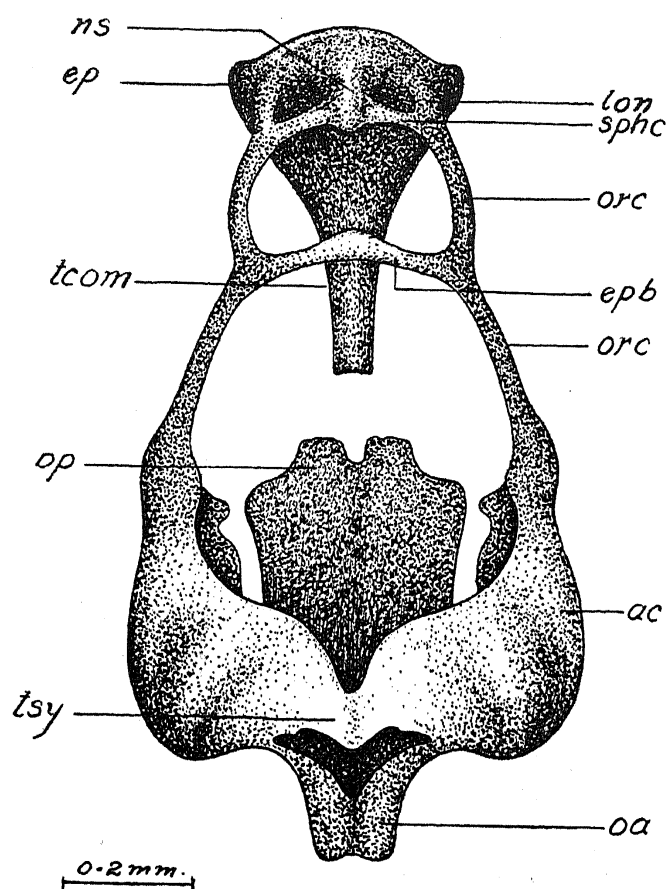


FIG. 8. Dorsal view of the chondrocranium of *T. trichopterus*, stage 9. Total length of larval form 6.0 mm. (model). The visceral arches and the ossified portions are not shown.

The basivestibular commissure (Fig. 14, *bvc*) is quite prominent and the head vein lies ventral to it. The occipital region is without a roof.

The pterygoid process (Figs. 10 and 11, *ptp*) articulates with the ventrolateral side of the ethmoid plate. The quadrate part of the pterygoquadrate cartilage (Fig. 10, *qu*) is broad and gives articulation to Meckel's cartilage ventrally. Part of the hyosymplectic cartilage anterior to the opening of the hyomandibular foramen is ossified (Fig. 10, *hs*). The remaining elements of the hyoid arch (Fig. 11) are well developed.

The first copula (Fig. 11, *cop 1*) is continuous in front with the basihyal (*bh*). Immediately behind the basihyal, it enlarges into a large vertical plate and then divides into two parts, a dorsal and a ventral in the region of the first branchial arch (Fig. 11, *cop 1*). The dorsal part extends behind upto the second copula and the ventral runs posteriorly for a short distance. The first copula (*cop 1*) gives attachment to the first three pairs of branchial arches

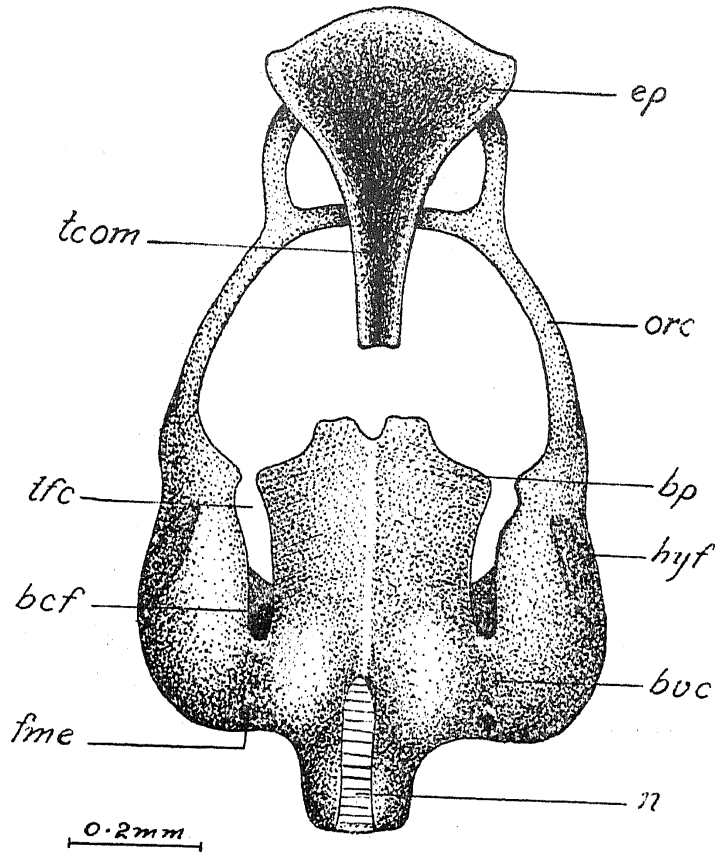


FIG. 9. Ventral view of the chondrocranium of stage 9 (model).

and the second to the remaining two. However, it is interesting to note that the third hypobranchial (*hb* 3) is connected with the second copula as well. Only the first epibranchial (*eb* 1) can be seen as an independent cartilage, as

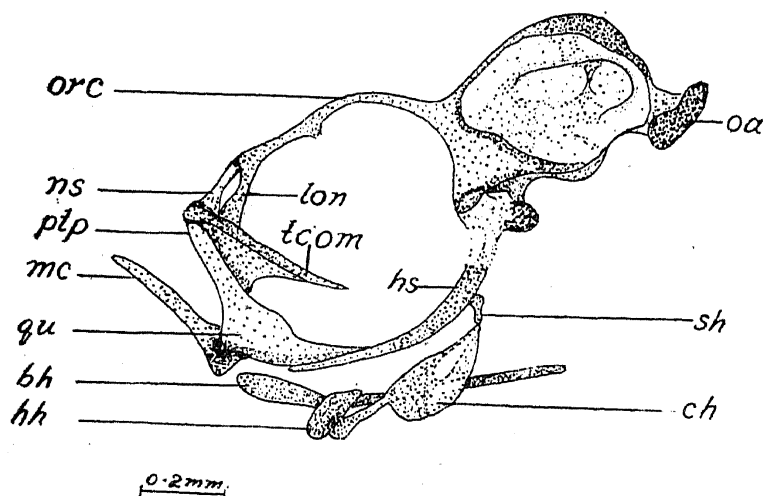


FIG. 10. Lateral view of the chondrocranium of *T. trichopterus* of stage 9 (van Wijhe's technique). Branchial arches are not shown.

the remaining epibranchials are not differentiated in this stage. The first three pharyngobranchials are clearly seen and they are supported by muscles

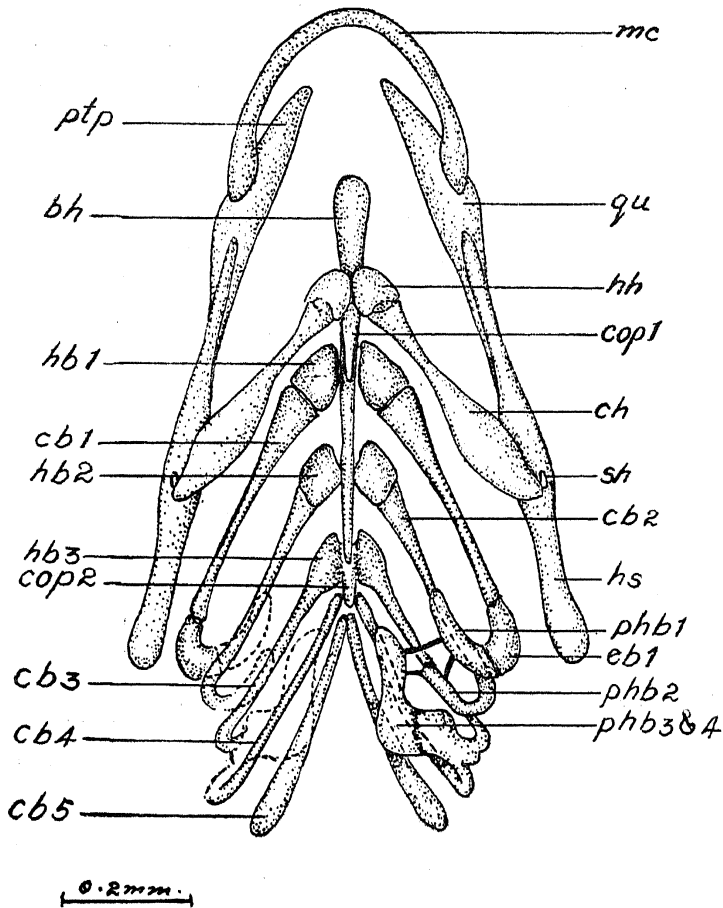


FIG. 11. Dorsal view of the visceral arches of *T. trichopterus*, stage 9 (model).

from the ventral wall of the auditory capsule. The first two pharyngobranchials (*phb* 1 and 2) are comparatively smaller than the third (*phb* 3 and 4) which is connected with the third and the fourth branchial arches. It appears to be formed by the fusion of the third and the fourth pharyngobranchials.

Stage 10 (Total length 11.5 mm.) (Figs. 12-18).—*Morphology of the fully formed chondrocranium.*—

(a) *Cranium*

1. *The ethmoid region* (Figs. 12-15).—This region is well developed and consists of a prominent ethmoid plate, a nasal septum and a pair of laminae orbitonasales. A rostral cartilage is not noticed in this fish,

The ethmoid plate (*ep*) is round anteriorly and bears ventrally a shallow depression or groove; dorsally is seen a large nasal septum (*ns*) which is broader than in previous stages. It is connected posteriorly to the sphenoseptal commissure of the orbital cartilage. The lamina orbitonasalis (*lon.*) is in contact with the posterolateral side of the ethmoid plate and its dorsal end merges with the orbital cartilage. The olfactory foramen is bordered laterally by the lamina orbitonasalis and medially by the nasal septum.

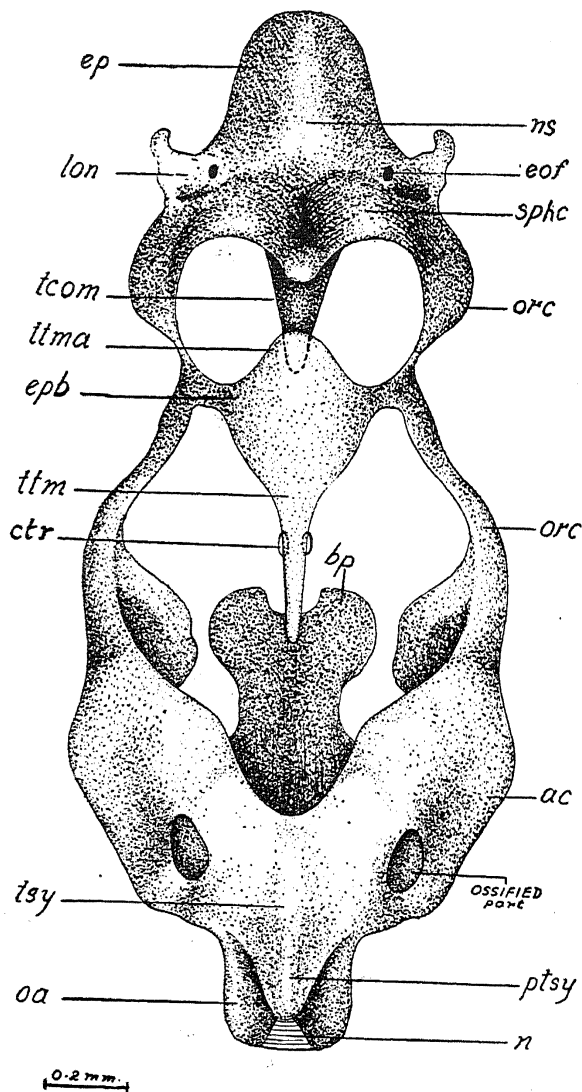


FIG. 12. Dorsal aspect of the chondrocranium of *T. trichopterus*, stage 10. Total length of larva 11.5 mm. (model). The visceral arches are not shown.

In this fish the brain extends very much anteriorly within the cranial cavity and hence the olfactory nerve after emerging out of the chondrocranium

through the olfactory foramen innervates immediately the olfactory sac. The foramen olfactorium advehens of *Salmo* (de Beer, 1937) is not noticed in this fish and hence the olfactory foramen may be called the foramen olfactorium evehens. This foramen is traversed by the orbitonasal artery

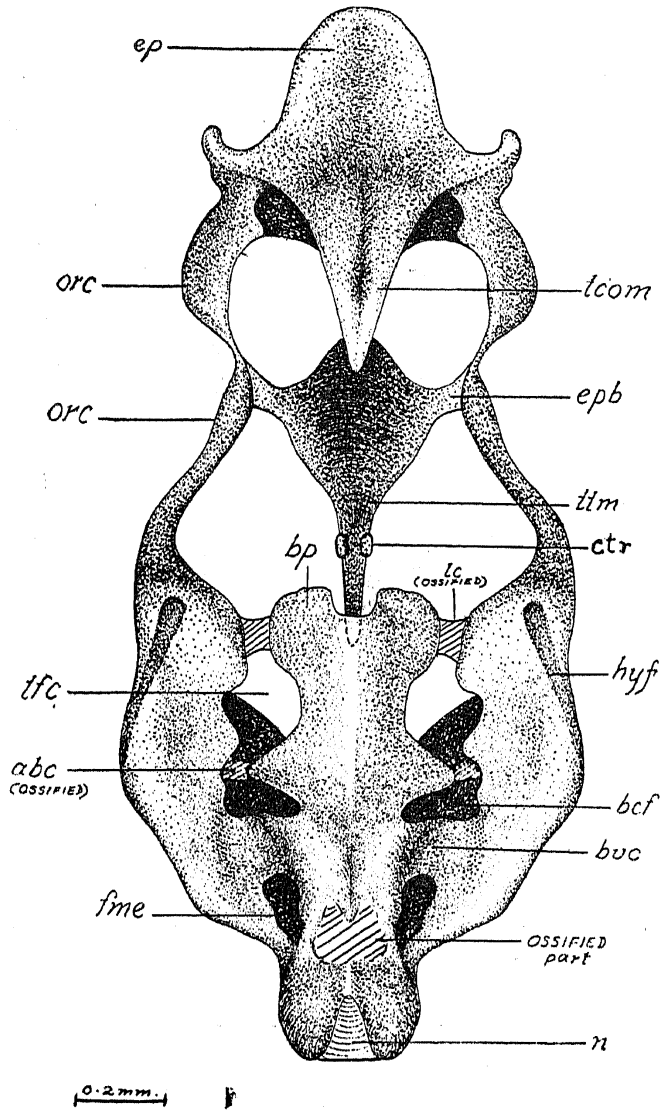


FIG. 13. Ventral view of the chondrocranium of stage 10 (model).

in addition to the olfactory nerve. The olfactory sac is not covered by any cartilage either dorsally or laterally. Even on the ventral side there is no direct cartilaginous support as the sac is placed at a much higher level than the ventral ethmoid plate.

2. *The orbito-temporal region* (Figs. 12-17).—Posterior to the ethmoid plate, the trabecula communis is seen (Figs. 12-14, *tcom*) running in a postero-

ventral direction. As pointed out in the previous stage it does not reach the basal plate, resulting in the obliteration of the hypophysial fenestra. It is quite broad in front and tapers behind. Ventrally the trabecula communis shows a distinct median groove running throughout its length and continues with the shallow depression of the ethmoid plate. This groove lodges the parasphenoid bone.

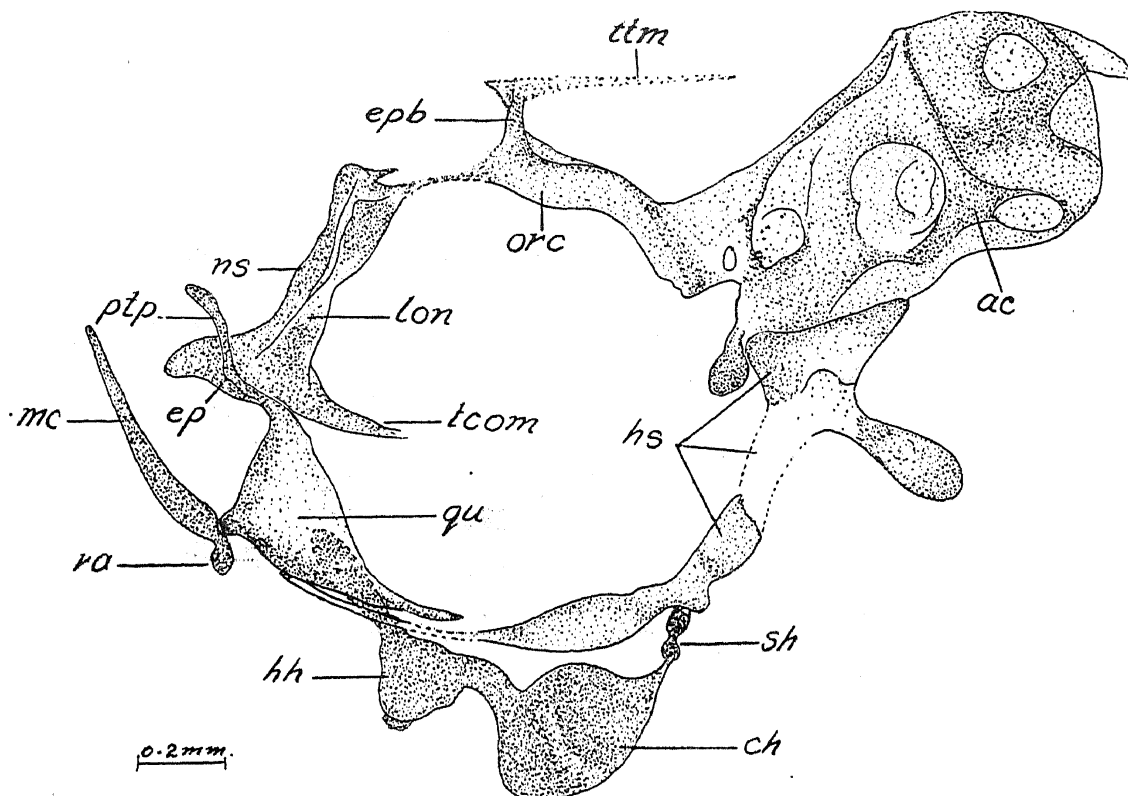


FIG. 14. Lateral view of the chondrocranium of *T. trichopterus*, total length 12.0 mm. (van Wijhe's technique). Branchial arches are not shown.

The well-developed and elongated orbital cartilage or tænia marginalis is seen extending between the auditory capsule and the ethmoid region. It joins the epiphysial cartilage near its middle, in front of which it is quite thin for a short distance and anteriorly it develops into a broad massive cartilage uniting in front with the lamina orbitonasalis and also with the nasal septum through its median sphenoseptal commissure. The sphenoseptal commissures from the two sides unite in the middle and form a prominent roof over the anterior region of the brain (Fig. 12, *sphc*). This roof has a distinct median groove with an arched portion on either side. Posteromedially the roof is produced into a small blunt process which does not reach the tænia tecti medialis anterior.

The epiphysial cartilage (Fig. 12, *epb*) is very well developed and is quite large. It extends anteriorly and posteriorly into tænia tecti medialis. The posterior extension is triangular in shape and forms a roof of the brain in this region.

A membranous inter-orbital septum is present and it generally limits the anterior and ventral extension of the brain in fishes. In *Trichopodus* it, however, limits the ventral extension of the brain. The septum is

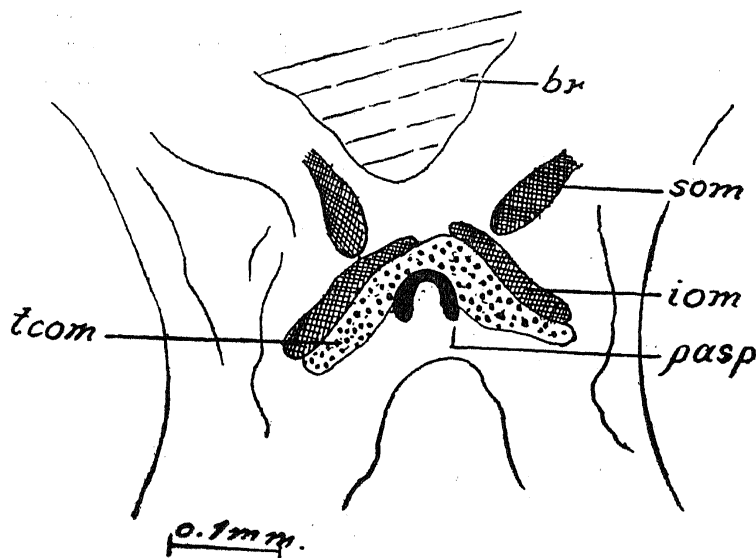


FIG. 15.

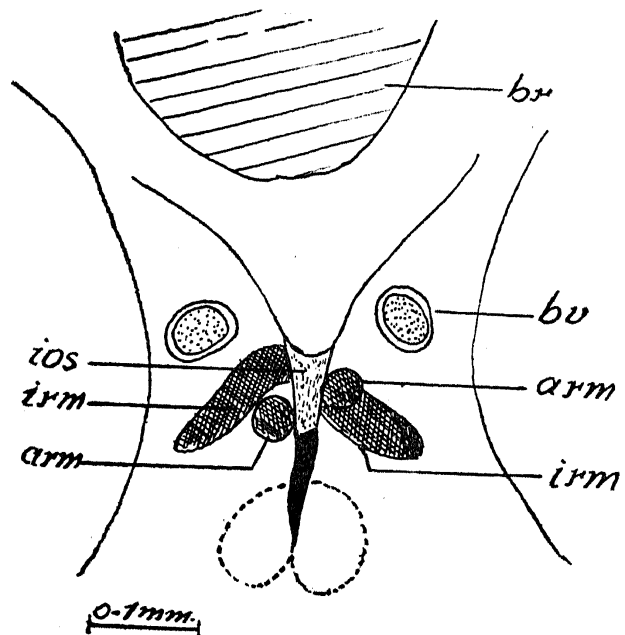


FIG. 16.

ventrally attached to the trabecula communis and behind it to the parasphenoid bone. Dorsally it is attached throughout its length to the membranous floor (dura mater) of the brain-cavity. Anteriorly the inter-orbital septum is quite thick and broad and is formed of connective tissue. It then gradually becomes laterally compressed into a narrow partition. Further behind, its lower part is reduced giving it a somewhat triangular appearance. In the posterior-most part, the septum though thin increases in height and joins the parasphenoid bone.

The oblique eye-muscles (Fig. 15, *som* and *iom*) are attached to the dorsal margin of the trabecula communis (*tcom*) even before the formation of the inter-orbital septum. The point of attachment of the superior oblique muscle is slightly anterior to that of the inferior. There is no anterior eye-muscle canal as in *Clupea* (Norman, 1926).

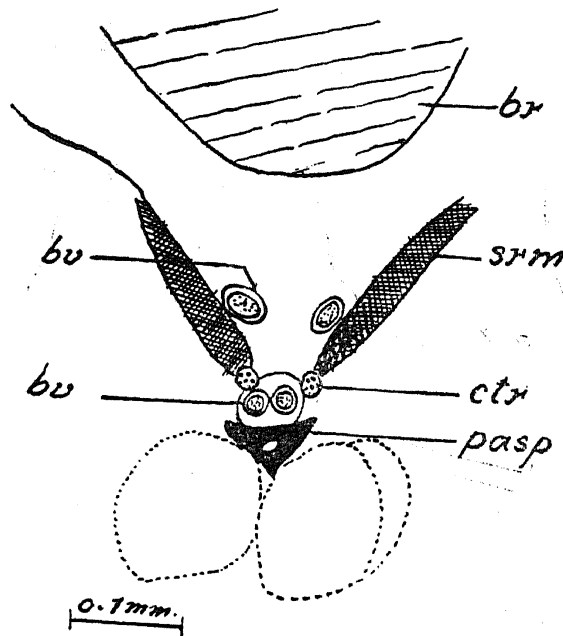


FIG. 17.

Figs. 15-17. Transverse sections of *T. trichopterus*, stage 10.

The anterior and inferior recti-muscles join the inter-orbital septum (Fig. 16, *arm* and *irm*). The point of attachment of the inferior rectus muscle is situated dorsal to that of the anterior on one side and *vice versa* on the other. In addition the inferior rectus muscle is attached posteriorly to the thin wall of the brain-cavity.

The superior rectus muscle (Fig. 17, *srm*) runs beyond the point of attachment of the inferior rectus and is attached to a small rod-like cartilage (*ctr*).



This short cylindrical cartilage is not noticed in earlier stages. These paired cartilages together with the ventrally placed parasphenoid, form a small chamber, enclosing the internal carotid arteries. The superior rectus muscle after its attachment with the above cartilage extends behind for over 20 micra.

The posterior rectus muscle runs beyond the rod-like cartilage and is attached to the thin membranous ventral wall of the brain-cavity. This membranous wall also forms the roof of the chamber lodging the internal carotid arteries. In this region the parachordals are seen as small independent cartilaginous rods forming the lateral walls of the chamber. The two internal carotid arteries are separated from one another by a connective tissue septum.

An independent complete ring of sclerotic cartilage is developed around each eye.

Both lateral and anterior basicapsular commissures are ossified as noticed in the previous stage. A few cartilaginous cells are seen scattered inside the ossified commissures. The branches of the trigeminal nerve leave the cranium in front of the lateral commissure. The facial ganglion is distinct and is situated slightly ventral and medial to the head vein. The palatine nerve is also placed medial to the head vein but situated anterior to the other branches of the facial nerve. It starts from the brain as an independent branch and leaves the cranium along with the branches of the trigeminal nerve in front of the ossified lateral commissure.

3. *Auditory capsules* (Figs. 12-14).—The auditory capsules (*ac*) are separated from the brain-cavity by a thin membrane as in *Salmo* (de Beer, 1937) and *Gambusia* (Ramaswami, 1945). The auditory sacs are surrounded by cartilage and the outer cartilaginous wall of the lateral and posterior semicircular canals is partly ossified.

This ossified region has been noticed as a definite cartilage in the previous stage (6 mm. larva). The abovementioned two canals are raised and hence their boundaries can be clearly made out externally. Internally, the semicircular canals are separated from the brain-cavity by two cartilaginous septa—the septum semicircularis lateralis and the septum semicircularis posterior. The former septum is a prominent pillar-like cartilage, disposed slightly obliquely. The latter which separates the posterior semicircular canal is vertical and not prominent. The anterior semicircular canal is not separated from the brain-cavity by any septum. The auditory capsular cartilages extend dorsally as the tectum synoticum, covering the hind brain

(Fig. 12, *tsy*). Posteriorly, the tectum extends over the occipital region as a conical process (Fig. 12, *ptsy*). The head of the hyosymplectic cartilage fits in a groove on the ventral side below the bulge of the lateral semi-circular canal (Fig. 13, *hyf*).

4. *The occipital region* (Fig. 12).—A pair of occipital cartilages (*oa*) is noticed in the posterior part of the chondrocranium and each one of them is continuous anteriorly with the corresponding auditory capsule. Posteriorly they are very much reduced and lie on the dorsolateral side of the notochord.

5. *The basal plate* (Figs. 12 and 13).—The basal plate (*bp*) is well developed and extends medially between the orbito-temporal and the occipital regions. Anteriorly it shows a distinct notch, marking the posterior boundary of the original hypophysial fenestra. The lateral and the anterior basicapsular commissures are ossified as already stated. The basivestibular commissure (Fig. 13, *bvc*) is well represented and the metotic foramen (*fme*) situated behind it serves as a common exit for the glossopharyngeal and vagus nerves. The metotic foramen is slightly ossified. Near its posterior end a median part of the basal plate is ossified as shown by a gap in the figure.

6. *The notochord*.—In this stage the notochord which is much reduced extends into the cranium for a short distance. Ventrally it is exposed throughout its length. Dorsally it is covered in front by the basal plate and the remaining part is visible between the occipital arch elements.

(b) *Visceral arches*

7. *The mandibular arch*.—The mandibular arch, consisting of an upper pterygoquadrate and a lower Meckel's cartilage is now fully formed.

(i) *The pterygoquadrate (the palato-quadrate)* (Fig. 14).—It consists of an extensive quadrate part (*qu*) giving articulation ventrally to Meckel's cartilage (*mc*). It has a posterior process extending over a ventral part of the hyosymplectic cartilage with which it does not unite. The pterygoid process (*ptp*) is a slender bent cartilaginous piece, running in front dorsal to the ethmoid plate. As there is no special ethmopalatine process it articulates directly with the ethmoid plate.

(ii) *Meckel's cartilage* (Fig. 14).—The rod-like Meckel's cartilage (*mc*) is disposed obliquely and extends anteriorly beyond the ethmoid plate. The anterior symphysis of Meckel's cartilages is ossified and is replaced by dentaries. Posteriorly Meckel's cartilage extends behind the point of articulation with the pterygoquadrate as a small knob-like retroarticular process (*ra*).

8. *The hyoid arch* (Figs. 14 and 18).—The well developed, rod-like, basihyal (Fig. 18, *bh*) extends anteriorly upto the level of the ethmoid region and continues behind with the basibranchial. The two hypohyals (Figs. 14 and 18, *hh*) are stout cartilages which partially encircle the basihyal. They are not perforated by the hyoidean artery nor are they delimited from the ceratohyals.

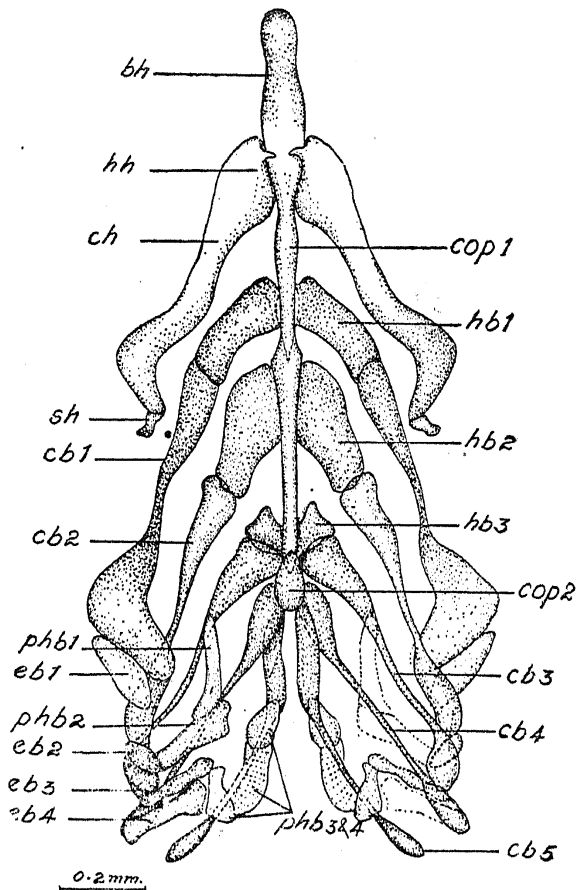


FIG. 18. Dorsal view of the hypobranchial skeleton of *T. trichopterus*, stage 10 (model). Hyomandibular and symplectic are not shown.

The ceratohyals (*ch*) are slightly bent, elongated cartilages, quite broad in their posterior half. They extend anteriorly below the hypohyals with which they are firmly united. The stylohyal (*sh*) is a small dumbel-shaped cartilage, connected dorsally to the hyosymplectic and ventrally to the ceratohyal.

Ossification has set in the hyosymplectic cartilage (Fig. 14, *hs*) in the region of the hyomandibular foramen. The head of the hyosymplectic abuts against the ventrolateral side of the chondrocranium in the auditory region and extends from the lateral commissure to the basicapsular fenestra.

A distinct rod-like cartilage arises from the upper part of the hyosymplectic and runs posteriorly to give attachment to the opercular bone.

The lower portion of the hyosymplectic is elongated and extends ventrally below the quadrate. Perichondral ossification is noticed in this region. It supports the stylohyal in a notch near its upper part.

9. *The branchial arches* (Fig. 18).—All the five pairs of branchial arches are present. The first three arches show all the elements namely the hypo-cerato-, epi-, and pharyngo-branchials. The fourth arch has a common hypo-ceratobranchial and the pharyngobranchials of the third and fourth arches are united. The fifth arch consists of only the ceratobranchials. Ossification has already set in and a major part of the cartilage from the middle part of the ceratobranchial is ossified.

The basibranchials unite to form the median copulæ, to which the hypo-branchials or ceratobranchials are united. In this fish there are two distinct copulæ (*cop 1* and *cop 2*) an anterior and a posterior. The anterior copula (*cop 1*) is very much elongated and gives attachment to the first three hypo-branchials. As pointed out in the previous stage (6.0 mm. larva), the first copula consists of two parts a short ventral and an elongated dorsal piece. The posterior copula (*cop 2*) is short and supports the ceratobranchials of the third arch and the hypo-ceratobranchials of the fourth arch. The fifth arch (*cb 5*) is being ossified and is connected with the second copula through a ligamentous tissue. All the four epibranchials (*eb 1-4*) are well developed the second being the shortest.

The first two pharyngobranchials (*phb 1* and *2*) are rod-shaped and smaller in size than the common third and fourth pharyngobranchial (*phb 3* and *4*) which is ossified in the middle.

#### DISCUSSION

In fish the trabeculæ arise from the mesenchymatous plaques which are in contact with the epidermis and they are continuous with the mesenchyme of the mandibular arch (de Beer, 1931). A transverse commissure connects the two mandibular somites in *Salmo* (de Beer, 1931) which is absent in *Ophicephalus* (Srinivasachar, 1953). In *Trichopodus* the trabecular rudiments appear as rod-like procartilages in a 2.4 mm. larva and the mesenchymatous plaques described by de Beer or the mesenchymatous tracts recorded by Srinivasachar cannot be made out. The appearance of mesenchymatous tracts in the development of *Trichopodus* may have been skipped due to the shortened larval life.

The time of appearance of the trabeculæ in relation to that of parachordals varies in different teleosts. The trabeculæ appear to develop earlier than the parachordals in *Salmo* (Stohr, 1882), *Lepidosiren* and *Protopterus* (Agar, 1908). In *Sebastes* (Mackintosh, 1923) the trabeculæ are laid down as definite tracts of procartilage even when there is no trace of parachordals. The parachordals appear earlier than the trabeculæ in *Salmo* (de Beer, 1927), *Acipenser* (Sewertzoff, 1928) and *Polypterus* (Moy Thomas, 1933). In *Ophicephalus* (Srinivasachar, 1953) the two elements seem to develop simultaneously.

In the case of *Trichopodus* the trabeculæ seem to form slightly earlier than the parachordals, because the trabeculæ are better represented in a 2.4 mm. larva (Stage 1) than the parachordals.

In many teleosts the trabeculæ behind the ethmoid plate fuse medially to form a trabecula communis but posteriorly they are free and continuous with the parachordals, enclosing a small hypophysial fenestra. This type of cranium is called the tropitrabic cranium and generally possesses an inter-orbital septum as in *Syngnathus* (Kindred, 1921), *Clupea* (Wells, 1922), *Sebastes* (Mackintosh, 1923), *Anguilla* (Norman, 1926) and *Salmo* (de Beer, 1927).

In fishes like *Gasterosteus* (Swinnerton, 1902), *Gymnarchus* (Assheton, 1907), *Amiurus* (Kindred, 1919) and *Amia* (Pehrson, 1922) the cranium is of the platytrabic type where the trabeculæ remain apart and the inter-orbital septum is absent. In *Ophicephalus* (Srinivasachar, 1953) a trabecula communis is present but no inter-orbital septum is formed. It is also called the platytrabic type of cranium.

The cranium of *Trichopodus* belongs to the tropitrabic type as the trabecula communis as well as the inter-orbital septum are present.

Generally one or more fenestræ are present in the floor of the chondrocranium and they may or may not be closed by cartilage or bone at a later stage. In the platytrabic type of cranium there is a single large hypophysial fenestra and the notochord projects into it. In *Lepidosteus* (Veit, 1911) and *Amia* (Pehrson, 1922) this fenestra shows two broad sections, an anterior and a posterior.

In the tropitrabic cranium the hypophysial fenestra is present but it is smaller than in the platytrabic type. It may be divided into anterior and posterior compartments due to the widening of the bordering cartilage as in *Gasterosteus* (Swinnerton, 1902) and *Salmo* (de Beer, 1927).

In *Gymnarchus* (Assheton, 1907) and *Anguilla* (Norman, 1926) a narrow internal carotid foramen is separated off from the hypophysial fenestra.

In *Trichopodus* the hypophysial fenestra is small and triangular in outline. In later stages the fenestra is obliterated due to the absorption of the posterior part of trabeculæ, as noticed in *Gambusia* (Ramaswami, 1945) and *Ophicephalus* (Srinivasachar, 1953).

The laminae orbitonasales arise as upgrowths from the posterolateral edges of the ethmoid plate and dorsally fuse with the anterior ends of the orbital cartilages or with the nasal septum. They form the outer bounding wall for the olfactory foramen. When the lamina orbitonasalis is broad and massive as in *Cyclopterus* (Uhlmann, 1921) and *Salmo* (de Beer, 1927) the olfactory foramen is comparatively reduced and when small the olfactory foramen is large as in *Anguilla* (Norman, 1926). This shows that the size of the olfactory foramen is determined by the size of the lamina orbitonasalis.

In *Cyclopterus* (Uhlmann, 1921) the lamina orbitonasalis seems to arise from two centres of chondrification, a ventral and a dorsal. Procartilage is formed between these two centres. Later, the two centres grow and fuse with each other. In *Syngnathus* (Kindred, 1921) the laminae orbitonasales do not meet the ventral ethmoid plate and this is considered as a secondary modification. In *Trichopodus* the lamina orbitonasalis develops as an upgrowth from the posterolateral side of the ethmoid plate.

The foramen through which the olfactory nerve enters the nasal cavity may not be the same as the one through which the olfactory nerve leaves the cranial cavity (de Beer, 1937). The foramen leading the olfactory nerve out of the true cranial cavity is called foramen olfactorium evehens. It is bounded posteriorly by the preoptic root of the orbital cartilage, ventrally by the ethmoid plate, anteriorly by the nasal septum and dorsally by the sphenoseptal commissure.

The olfactory foramen in fishes like *Polypterus* (Moy Thomas, 1933), *Acipenser* (Sewertzoff, 1928), *Gadus* (de Beer, 1937) opens directly into the nasal cavity. But in other fishes such as *Salmo* (de Beer, 1927), *Lepidosteus* (Veit, 1911) and *Amia* (Pehrson, 1922), due to the backward shifting of the pre-optic root or due to the forward movement of the lamina orbitonasalis, the foramen olfactorium evehens no longer opens directly into the nasal cavity, but into an extracranial space the cavum orbitonasale. This space is also traversed by the nasal branch of the profundus nerve and the orbitonasal artery. The cavum orbitonasale opens anteriorly into the nasal cavity by a wide mouthed opening, the foramen olfactorium advehens, bounded laterally by the lamina orbitonasalis, medially by the nasal septum and ventrally by the ethmoid plate.

In *Ophicephalus* (Srinivasachar, 1953) the foramen olfactorium evehens and advehens are said to be confluent.

In *Trichopodus* the brain extends anteriorly and the olfactory nerve after emerging out of the cranium through the foramen olfactorium evehens directly innervates the olfactory sac. The foramen olfactorium advehens is therefore absent.

The orbital cartilage gives rise in front to a sphenoseptal commissure joining the nasal septum as noticed in *Gasterosteus* (Swinnerton, 1902), *Salmo* (de Beer, 1927) and *Gambusia* (Ramaswami, 1945). In *Syngnathus* (Kindred 1921) the orbital cartilages are practically non-existent, excepting for the anterior and posterior ends in connection with the lamina orbitonasalis and the auditory capsule respectively.

In *Trichopodus* orbital cartilages are complete and well developed. The sphenoseptal commissure is also present.

The manner in which the supra-orbital bars appear in different teleosts is not uniform. In *Clupea* (quoted by Norman, 1926) each bar arises as an outgrowth from the anterior end of the auditory capsule and eventually reaches the anterior part of the cranial roof. In *Gasterosteus* (Swinnerton, 1902) and *Cyclopterus* (Uhlmann, 1921) the orbital cartilages appear to be interconnected with the epiphysial bar. They soon unite anteriorly with the laminae orbitonasales and posteriorly with the post-orbital process of the auditory capsules.

In *Amia* (Pehrson, 1922) a pair of small orbital cartilages is developed. Each one of them unites in front with a posterior process of the lamina orbitonasalis and behind with the auditory capsule. The epiphysial cartilage appears independently. In *Trichopodus* the orbital cartilages develop in association with the epiphysial bar, in a 3.5 mm. larva (Stage 7). In later stages they extend and join the laminae orbitonasales and the nasal septum anteriorly and the auditory capsules posteriorly.

The lateral commissure in *Salmo* (de Beer, 1927) is formed by the union of two processes, the post-palatine process arising from the anterolateral side of the basal plate and the pro-otic process coming from the anterior side of the auditory capsule. According to Norman (1926) the lateral commissure seems to arise as a projection from the lower edge of the thickened anterior end of the auditory capsule. This projection grows inwards between the roots of the fifth and seventh cranial nerves, finally fusing with the anterior end of the basal plate.

In *Ophicephalus* (Srinivasachar, 1953) a massive pro-otic cartilage and a slender post-palatine process are observed. These two cartilages do not meet and consequently the lateral commissure remains incomplete. In *Trichopodus* the lateral commissure appears in a 4.0 mm. larva as a thin slender plate-like structure forming the anterior boundary of the trigemino-facialis chamber. The pro-otic and the post-palatine processes are not found in the earlier forms examined.

The branches of the trigeminal as well the palatine branch of the facial run anterior to the lateral commissure. The remaining branches of the facial nerve lie within the trigeminofacialis chamber. The lateral commissure is ossified in a 6.0 mm. larva of *Trichopodus*.

In a 10.5 mm. larva of *Salmo fario* (de Beer, 1927) the cartilaginous rudiments of the auditory capsules are differentiated in the anterolateral corners of the otic-sacs and are connected with the anterior portion of the parachordals by a dense pro-cartilage. In *Gasterosteus* (Swinnerton, 1902) the auditory cartilage arises along with the parachordal and is never independent. Swinnerton (1902, p. 511) states that the stages during which the otic elements should be independent seem to be completely suppressed probably due to some influence at work hastening the development of that particular region. In *Trichopodus* the otic cartilage seems to appear slightly later than the parachordal as seen in stage one. Definite rudiments of the auditory cartilages appear a short time after and are connected with the parachordals by two commissures. This tends to show that the otic capsule is never independent though appearing slightly later than the parachordal. The fully formed auditory capsule generally shows external demarcation of the anterior, lateral and posterior semicircular canals in the teleosts. Internally the auditory capsule possesses one to three semicircular septa or partitions. In *Gobius* as stated by Norman (1926, p. 433) the lateral semicircular septum is chondrified, the posterior is fibrous and the anterior absent. Only two septa are seen in *Gasterosteus* (Swinnerton, 1902), *Syngnathus* (Kindred, 1921), *Cyclopterus* (Uhlmann, 1921), *Anguilla* (Norman, 1926), *Gambusia* (Ramaswami, 1945) and *Ophicephalus* (Srinivasachar, 1953). The anterior semicircular septum is absent.

In *Trichopodus* only two semicircular septa, namely the lateral and posterior, are present. The lateral septum which is generally vertical is a stout pillar-like cartilage, disposed slightly obliquely. The posterior septum is not very prominent.

The tectum synoticum unites the two auditory capsules dorsally in a number of teleosts like *Gasterosteus* (Swinnerton, 1902) *Cyclopterus*



(Uhlmann, 1921), *Anguilla* (Norman, 1926), *Salmo* (de Beer, 1927), *Gambusia* (Ramaswami, 1945) and *Ophicephalus* (Srinivasachar, 1953). In *Amiurus* (Kindred, 1919) the tectum synoticum is in continuation with the tectum posterius. In *Syngnathus* (Kindred, 1921) the tectum synoticum is very slender and is restricted only to the anterior region of the auditory capsules. A well developed tectum synoticum is present in *Trichopodus* and it extends posteriorly as a median conical process over the occipital region.

The auditory capsule is always connected with the anterior part of the parachordal by means of a cartilaginous bar, the anterior basicapsular commissure, situated behind the exit of the facial nerve in teleosts. Another commissure called the posterior basicapsular commissure is found between the exits of the glossopharyngeal and the vagus and it is present in *Amiurus* (Kindred, 1919), *Anguilla* (Norman, 1926) and *Salmo* (de Beer, 1927). A basicapsular fenestra is noticed between the two commissures. In these forms the exit of the vagus is through the jugular foramen and that of the glossopharyngeal is associated with basicapsular fenestra. In *Clupea* (Wells, 1922), *Gasterosteus* (Swinerton, 1902), *Gambusia* (Ramaswami, 1945) and *Ophicephalus* (Srinivasachar, 1953) the glossopharyngeal and the vagus leave the cranium through a common aperture the metotic foramen, separated from the basicapsular fenestra by a basivestibular commissure. This is also true in the case of *Trichopodus*.

In *Clupea* (Wells, 1922) and *Sebastes* (Mackintosh, 1923) the mandibular arch arising originally as a continuous cartilaginous or pro-cartilaginous element, differentiates subsequently into the quadrate and Meckel's cartilage. Norman (1926) who later examined these two fishes states that a distinct suture is observed between Meckel's cartilage and quadrate. In *Gasterosteus* (Swinerton, 1902), *Lepidosteus* (Veit, 1911), *Amia* (Pehrson, 1922), *Anguilla* (Norman, 1926) and *Salmo* (de Beer, 1927) the two elements of the mandibular arch arise as independent chondrifications.

In *Ophicephalus* (Srinivasachar, 1953) the pterygoid process of the pterygoquadrate bar appears as an independent piece of cartilage in 4.5 mm. larva and is situated on either side of the middle region of the ethmoid plate. It gradually extends posteriorly and in 6 mm. larva fuses with the quadrate. In the 24 mm. larva it again becomes discontinuous with the quadrate.

In *Trichopodus* the pterygoid process appears as an anterior extension of the quadrate and extends up to the ethmoid plate in a 4 mm. larva (stage 8). In a fully formed chondrocranium the pterygoid process is continuous with the quadrate and extends dorsal to the ethmoid plate,

The different elements of the hyoid arch chondrify independently in *Gasterosteus* (Swinnerton, 1902), and *Salmo* (de Beer, 1927). In *Lepidosteus* (Veit, 1911) and *Amia* (Pehrson, 1922) the symplectic arises as an independent chondrification in a continuous procartilaginous tract. In *Clupea* (Wells, 1922) and *Ophicephalus* (Srinivasachar, 1953) the quadrate fuses with the hyomandibular and remains continuous with it. In *Clupea* (Norman, 1926) the quadrate becomes independent of the hyosymplectic in a 30 mm. larva but in *Ophicephalus* (Srinivasachar, 1953) it is continuous with the hyomandibular even in the fully formed chondrocranium.

In *Trichopodus* the hyosymplectic appears as a continuous rod of cartilage in a 2.5 mm. larva (stage 2). The symplectic cartilage is at no stage free from the hyomandibular and hence, a hyosymplectic is present in the fully formed chondrocranium. The hyosymplectic ventrally touches the quadrate part of the palatoquadrate cartilage but does not fuse with it at any stage. The ceratohyal is also present but not directly connected with the hyosymplectic. According to Norman (1926) the interhyal (stylohyal) may be regarded as a new structure developed in correlation with the need for a stronger suspensorium for the remainder of the hyoid arch after the hyomandibular has moved forward. In *Lepidosteus* (Veit, 1911) and *Amia* (Pehrson, 1922) it develops as a separate cartilage in the ligament connecting the hyomandibular with the ceratohyal. The stylohyal is segmented off from the upper portion of the ceratohyal in *Salmo* (de Beer, 1927). In *Trichopodus* a procartilaginous stylohyal is noticed in a 2.8 mm. larva (Stage 2) and it is chondrified in the next stage.

The basihyal is chondrified independently of the copula in *Gasterosteus* (Swinnerton, 1902) but is connected with it by pro-cartilage. In *Trichopodus* the basihyal does not arise as an independent chondrification but appears to be continuous with the first copula. Even in the fully formed chondrocranium it is continuous with the copula and expands into a stout rod-like cartilage anteriorly.

In *Ophicephalus* (Srinivasachar, 1953) there is an elongated common copula which gives attachment to all the five pairs of branchial arches. In *Gambusia* (Ramaswami, 1945) and many other teleosts generally there are noticed two copulae giving attachment to the different branchial arches. In *Trichopodus* two copulae are noticed. The branchial arches develop mostly in the same manner as in *Salmo* (de Beer, 1927) and *Ophicephalus* (Srinivasachar, 1953).

SUMMARY

Eighty stages were collected for the study of the development of the chondrocranium of *T. trichopterus* and ten of them have been studied in detail.

(a) The notochord is noticed in stage 1 (2.4 mm.).

(b) The trabeculæ and the parachordals make their appearance as procartilages in stage 1 (2.4 mm.).

(c) In stage 2 (2.5 mm.) the ethmoid plate is developed. The trabeculæ unite posteriorly with the parachordals enclosing a wide hypophysial fenestra. The anterior basicapsular and the basivestibular commissures are formed. Rudiments of the occipital arch elements are seen. Meckel's cartilage and quadrate part of pterygoquadrate cartilage are developed but they are not united with each other. Two basibranchials are seen and the anterior one unites with the basihyal.

(d) In stage 3 (2.8 mm.) a small procartilaginous stylohyal appears.

(e) In stage 4 (3 mm.) the stylohyal becomes cartilaginous and connects the ceratohyal with the hyomandibular. Two pharyngobranchials are noticed.

(f) In stage 7 (3.5 mm.) the orbital and epiphysial cartilages make their appearance. The orbital cartilage is placed between the ethmoid and auditory regions but is not connected to them in this stage. The first three pharyngobranchials are formed.

(g) In stage 8 (4 mm.) the trabecula communis is developed. The median nasal septum and the lamina orbitonasalis are appearing. The orbital cartilage unites with the auditory capsule. The lateral commissure is developed. The metotic foramen is formed. The pterygoid process extends anteriorly up to the ethmoid plate.

(h) In stage 9 (6 mm.) the nasal septum has united with the sphenoseptal commissure of the orbital cartilage. The trabeculæ become discontinuous with the parachordals; hence the boundary of the hypophysial fenestra is obliterated. The auditory capsule which is well developed shows internally two septa. A synotic tectum is formed. The first epibranchial is formed and the third and fourth pharyngobranchials are united.

(i) In the fully formed tropitric chondrocranium (stage 10; 11.5 mm.) the two sphenoseptal commissures unite in the middle, forming a roof for the brain. The tænia tecti medialis and tænia tecti medialis anterior are developed. A membranous inter-orbital septum is present. The oblique

eye-muscles are attached to the trabecula communis. The pterygoid process extends dorsal to the ethmoid plate. Meckel's cartilage has a retro-articular process. The basihyal is still continuous with the first basibranchial.

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KEY TO ABBREVIATIONS

|  |  |
|--|--|
| <i>abc</i> .. anterior basicapsular commissure                                   | <i>mc</i> .. Meckel's cartilage                                |
| <i>ac</i> .. auditory capsule  | <i>mcu</i> .. Rami of Meckel's cartilage united anteriorly     |
| <i>aep</i> .. anterior ethmoid process   | <i>n</i> .. notochord  |
| <i>arm</i> .. anterior rectus muscle   | <i>ns</i> .. nasal septum                                      |
| <i>arp</i> .. articular process  | <i>oa</i> .. occipital arch                                    |
| <i>ba</i> 1-5 .. branchial arches 1-5  | <i>orc</i> .. orbital cartilage                                |
| <i>bcf</i> .. basicapsular fenestra  | <i>pc</i> .. parachordal                                       |
| <i>bh</i> .. basihyal  | <i>phb</i> 1-4 .. pharyngobranchials 1-4                       |
| <i>bp</i> .. basal plate   | <i>pm</i> .. posterior myodome                                 |
| <i>br</i> .. brain   | <i>ppsc</i> .. prominence of the posterior semi-circular canal |
| <i>bvc</i> .. basivestibular commissure  | <i>ptp</i> .. pterygoid process                                |
| <i>cb</i> 1-5 .. ceratobranchials 1-5  | <i>ptq</i> .. pterygo quadrate                                 |
| <i>ch</i> .. ceratohyals   | <i>ptsy</i> .. posterior extension of tectum synoticum         |
| <i>cop</i> 1-2 .. copulae 1-2 or basibranchials 1-2                              | <i>qu</i> .. quadrate  |
| <i>ct</i> .. cartilage   | <i>ra</i> .. retroarticular process of Meckel's cartilage      |
| <i>ctr</i> .. cartilaginous rod  | <i>rc</i> .. rostral cartilage                                 |
| <i>eb</i> 1-4 .. epibranchials 1-4   | <i>rm</i> .. rectus muscle                                     |
| <i>emc</i> .. anterior eye-muscle canal  | <i>sh</i> .. stylohyal   |
| <i>eof</i> .. foramen olfactorium evehens  | <i>som</i> .. superior oblique muscle                          |
| <i>ep</i> .. ethmoid plate   | <i>sphc</i> .. sphenoseptal commissure                         |
| <i>epb</i> .. epiphysial bar   | <i>ssl</i> .. septum semicircularis lateralis                  |
| <i>fh</i> .. foramen in the hyosymplectic for the hyomandibularis facialis nerve | <i>ssp</i> .. septum semicircularis posterius                  |
| <i>fme</i> .. metotic foramen  | <i>tc</i> .. trabecula   |
| <i>hb</i> 1-3 .. hypobranchials 1-3  | <i>tcom</i> .. trabecula communis                              |
| <i>hh</i> .. hypohyal  | <i>tfe</i> .. trigeminofacialis chamber                        |
| <i>hs</i> .. hyosymplectic   | <i>tsy</i> .. tectum synoticum                                 |
| <i>hyf</i> .. facet for the articulation of the hyosymplectic                    | <i>ttm</i> .. tænia tecti medialis                             |
| <i>iom</i> .. inferior oblique muscle  | <i>ttma</i> .. tænia tecti medialis anterior                   |
| <i>irm</i> .. inferior rectus muscle   |  |
| <i>lcm</i> .. lateral commissure   |  |
| <i>lon</i> .. lamina orbitonasalis   |  |