The Early Development of the Chondrocranium of *Salmo fario*.

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With 52 Text-figures.

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INTRODUCTION.

As in the case of most other forms, the development of the chondrocranium of the salmon and trout is best known during the later stages. Gaupp’s (1906) model, and his excellent description of it, are of a stage when the various cartilages have for the most part joined together and obscured their method of origin. Böker (1913) studied a stage still more advanced, and Schleip (1904) showed how the bones arise. For the earliest stages of development we are indebted to Parker (1873) and Stöhr (1882). Parker’s account, excellent as it is, cannot be
regarded as up to date, and in certain instances it can be shown to be inaccurate. Stöhr pointed out certain errors which Parker, with the methods then in use, was unable to avoid. There are, however, certain points in Stöhr’s account with which other workers have not agreed, and which are of sufficient importance to be worthy of investigation. The results described in this paper are the outcome of work primarily undertaken to determine three points: (a) whether the anterior parachordals described by Stöhr normally chondrify separately; (b) how the lateral commissure is formed, and the details of the processes of its formation; and (c) the details of formation of the hyoid and branchial arches.

For this purpose a large number (about three hundred) of preparations of embryos of Salmo fario was made by van Wijhe’s methods (1902 and 1922), using methylene blue and Victoria blue. The latter was found to give the best results; and I wish to record my gratitude to Professor van Wijhe for showing me what may be called the ‘type specimens’ of his method, in his laboratory in Groningen.

The embryos were obtained from the Berkshire trout farm, Hungerford. My thanks are due to Mr. Peart for the care which he took in supplying and dispatching them, which contributed greatly to the success of the investigation. The embryos were brought to Oxford four weeks after fertilization, and reared in the Department of Zoology and Comparative Anatomy. Hatching took place 48 days after fertilization (at room temperature), and the majority of embryos hatched together within a period of 48 hours. Some few, however, remained unhatched for some days longer. In the following account, the age of the embryo is counted from the middle of the period when most of the embryos hatched. It will be found, however, that age is not a sure criterion of degree of development, and neither is the length, measured from head to tail under a dissecting microscope with vernier-callipers. In some cases younger and shorter embryos are found to be further developed than older and longer ones, but these irregularities do not extend beyond certain limits.
The completeness of the series so obtained led to an extension of the field which these investigations were originally intended to cover. A number of drawings were made directly from the preparations with the help of the camera lucida, and these are intended to show the details of the development of the Salmonid skull from the earliest stage up to that described by Gaupp (1906). I am indebted to my wife for assisting in the preparation of these drawings for publication.

In addition, about fifty sets of serial sections were studied for the purpose of checking the results obtained from the other preparations, and determining the relations of the cartilages to the neighbouring vessels and nerves. For van Wijhe's method is so strictly specific for cartilage, that not only are vessels and nerves perfectly transparent and unstained, but even the notochord is (in most cases) invisible. The position of the notochord is of course easy to determine with regard to the parachordals, but the point to which it extends had to be inferred from sections of corresponding stages of development, and inserted into the drawings of the preparations.

Two sets of serial sections were reconstructed into blotting-paper wax models, to assist in determining the relations of the cartilages to the surrounding structures.

These investigations were carried out in the Department of Zoology and Comparative Anatomy, at Oxford. I take pleasure in expressing my thanks to Professor Goodrich, F.R.S., for his kindly interest and encouragement in the work.

**Description of Specimens.**

The following specimens have been selected from the preparations, and are arranged in order of degree of development.

Embryo 7 B 1. 6 days before hatching, 9-3 mm. long (Text-fig. 1). In this specimen the cartilaginous skull makes its first appearance in the form of paired cartilages which are the hind ends of the future parachordals. Chondrification is most advanced at the posterior end of these cartilages, in the region which will ultimately give rise to the occipital arches. From this point forwards, the cartilage becomes less distinct and
Salmo fario. 6 days before hatching, 9.3 mm. long, dorsal view (embryo 7 B 1).

EXPLANATION OF LETTERING.

abc, anterior basicapsular commissure; ac, auditory capsule; aof, advehent olfactory foramen; as, auditory sac; asc, anterior semicircular canal; bcf, basicapsular fenestra; bd, basidorsal; bf, basicranial fenestra; bh, basihyal; bp, basal process of pterygo-quadratus; cb 1–5, ceratobranchial 1 to 5; cg, ciliary ganglion; ch, ceratohyal; cn, ciliary nerve; cop, copula; ds, depression lodging the saccule; e, eye; eb 1–5, epibranchial 1 to 5; eof, evehent olfactory foramen; ep, ethmoid plate; eps, ethmo-palatine articulation; epb, epiphysial bar; eps, efferent pseudobranchial artery; er, external rectus muscle; f, facial nerve; fh, foramen in hyomandibular for facial nerve; fo, foramen for opthalmic nerve; g, glossohypophysyal nerve; gf, foramen for glossohypophysyal nerve; hb 1–4, hypobranchial 1 to 4; hf, hypophysial fenestra; hh, hypohyal; hm, hyomandibula; hv, head-vein; ic, internal carotid artery; id, interdorsal; infr, inferior rectus muscle; inr, internal rectus muscle; ins, internasal septum; io, inferior oblique muscle; ios, interorbital septum; ip, incisure for palatine nerve; jf, jugular foramen; ji, jugular incisure;
Salmo fario. 4 days before hatching, 9.5 mm. long, dorsal view (embryo 9 C 1).

lc, lateral commissure; lon, lamina orbito-nasalis; loc, lateral semicircular canal; mc, Meckel's cartilage; n, notochord; nh, notoch in hyomandibula for facial nerve; o, ophthalmic nerve; oa, occipital arch; oc, oculomotor nerve; of, foramen for olfactory nerve; om, ophthalmica magna artery; on, olfactory nerve; ona, orbito-nasal artery; onf, orbito-nasal fissure; op, otic process; opn, optic nerve; ova, orbital artery; os, olfactory sac; pb 1–2, pharyngobranchial 1, 2; pbc, posterior basicapsular commissure; pc, parachordal; pf, ramus palatinus facialis; pff, foramen for palatine nerve; ppp, post-palatine process; prb, prootic bridge; prp, prootic process; ps, pseudobranch; psc, posterior semicircular canal; ptp, pterygoid process of quadrate; pu, pituitary vein; qu, quadrate; r, rostrum; rac, roof of auditory capsule; rp, retro-articular process of Meckel's cartilage; rpa, rostro-palatine articulation; rpc, rudiment of parachordal; sh, stylohyal; so, superior oblique muscle; sp, septum of posterior semicircular canal; sr, superior rectus muscle; sy, symplectic; t, tectum; tc, trabecula cranii; tcom, trabecula communis; tm, taenia marginalis; tn, trigeminal nerve; tp, tectum synoticum; v, vagus nerve; vf, foramen for vagus nerve.
eventually fades into procartilage. There is no indication of separate anterior parachordal chondrification, but sections show that there is a dense region of procartilage in front of the anterior extremity of the parachordal cartilage. There is no sign of any other cartilage at this stage.

*Text-fig. 3.*

*Salmo fario.* 6 days before hatching, 9·6 mm. long, dorsal view (embryo 7 A 2).

Embryo 9 C 1. 4 days before hatching, 9·5 mm. long (*Text-fig. 2*). In this specimen the parachordal cartilages are not larger than in the preceding one, but they are denser and more thoroughly chondrified. The skeleton of the visceral arches has made its first appearance. The rudiments of Meckel's cartilages
and of the ceratohyals are present ventrally, while more dorsally in the hyoid arch the hyomandibula has appeared.

Embryo 7 A 2. 6 days before hatching, 9-6 mm. long (Text-fig. 3). The parachordals extend farther forward than in the previous stages, and this extension appears to be perfectly con-

Text-fig. 4.

Salmo fario. 8 days before hatching, 9-6 mm. long, dorsal view (embryo 5 A 1).

tinuous with the cartilage which first appeared. At the base of the extension the parachordals are marked by a swelling which shows the point where eventually the posterior basicapsular commissure will connect the auditory capsule to the parachordal. The hindmost region of the parachordals becomes produced into the occipital arches. These project upwards and outwards; their apparent asymmetry in some of the preparations and
drawings is due solely to the orientation of the specimen on the slide and to the point of view from which it is seen through the microscope.

Embryo 5 A 1. 8 days before hatching, 9.6 mm. long (Text-fig. 4). Here the trabeculae cranii have appeared as separate cartilages distinct from one another and from the parachordals. They lie to the side of and beneath the forebrain and diverge slightly as they run backwards. Close beneath them is the skin of the underside of the snout, but I find no evidence in support of Lundborg's (1899) view that the anterior region of the trabeculae (which gives rise to the ethmoid plate) is derived from the ectoderm.

Embryo 5 C 2. 8 days before hatching, 9.6 mm. long (Text-fig. 5). In this specimen the trabeculae have grown and extended farther backwards towards the parachordals, from which they are still distinct. Each trabecula is S-shaped, and the characteristic form of the future hypophysial fenestra (which
will be formed when the trabeculae and parachordals join) can already be recognized.

Embryo 6 B 3. 7 days before hatching, 9.3 mm. long (Text-fig. 6). This specimen, seen from the left side, shows that the trabeculae and parachordals arise more or less in the same plane. The hind end of the parachordal shows the beginning of the formation of the occipital arch.

Text-fig. 6.

Salmo fario. 7 days before hatching, 9.3 mm. long, left side view (embryo 6 B 3). The eye is shown with dotted lines.

Embryo 7 B 3. 6 days before hatching, 10 mm. long (Text-fig. 7). The visceral arches of these last and of some of the remaining stages are shown separately from the neurocranium, in order to avoid complicating the drawings. Not much advance has been made since the last stage described, but Meckel’s cartilages and the ceratohyals have grown longer.

Embryo 9 B 2. 4 days before hatching, 10 mm. long (Text-fig. 8). The trabecula and parachordal of each side have joined in this specimen, and the trabeculae are also extending farther forwards between the eyes. They are still widely separate from one another. There is no doubt that the normal method of
formation of the trabeculae is as just described, but occasionally exceptions are found. In one case the trabeculae appeared to be connected with the parachordals from the outset.
Embryo 7 A 2. 6 days before hatching, 10.2 mm. long (Text-fig. 9). The visceral arches show a considerable advance over preceding stages. Meckel's cartilages have extended forwards

**Text-fig. 9.**

Salmo fario. 6 days before hatching; 10.2 mm. long, ventral view of visceral arches (embryo 7 A 2).

Embryo 9 B 1. 4 days before hatching, 10 mm. long, left side view (embryo 9 B 1). The eye is shown with dotted lines. The mandibular arch for a considerable distance, but they do not meet one another. The first and second ceratobranchials have appeared, and also the quadrate.

Embryo 9 B 1. 4 days before hatching, 10 mm. long (Text-no. 282)
fig. 10). This stage is among the most important here described, and seen from the side it shows several interesting points. In the hyoid arch three separate cartilages are present: the hyomandibula, the symplectic, and the ceratohyal. The separate chondrification of the symplectic confirms Stöhr's (1882) account and contradicts Zanichelli's (1909). The quadrate and hyomandibula are quite separate and distinct, which is interesting in view of the close association in which these cartilages are reported to develop in Clupea by Wells (1923), in Sebastes by Mackintosh (1923), and to a much less intimate extent in Anguilla by Norman (1926). There can be no doubt that the condition in Salmo is primitive in this respect. (That portion of the hyomandibula which fuses with or touches the quadrate in these fish represents the symplectic.) The trabeculae and parachordals are joined to one another end to end.

Embryo 5 A 2. 8 days before hatching, 9.4 mm. long (Text-fig. 11). Here Meckel's cartilage is beginning to show the
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characteristic up-turned anterior end. The parachordals extend a little way back behind the base of the occipital arches. The quadrate and symplectic are almost touching, but the latter is still separate from the hyomandibula. The hyomandibula is extending as a thin sheet of cartilage upwards and backwards,

TEXT-FIG. 12.

Salmo fario. 5 days before hatching, 10-6 mm. long, dorsal view (embryo 8 C 1).

and it shows a distinct notch for the ramus hyomandibularis facialis. Edgeworth (1926) described the nerve as passing behind the primordium of the hyomandibula at first, and later becoming enclosed as the latter extends. This stage, therefore, shows the very act of enclosure. Berrill (1925) has described a similar process in the sole.
Embryo 8 C 1. 5 days before hatching, 10.6 mm. long (Text-fig. 12). In this specimen the auditory capsules have appeared, beneath the antero-lateral corners of the auditory sacs, and dorsal to the hyomandibulae. These auditory cartilages are connected with the anterior regions of the parachordals by dense procartilage.

Embryo 6. 2. 7 days before hatching, 10-2 mm. long (Text-fig. 13). The position of the auditory capsule in this specimen

**Text-fig. 13.**

Salmo fario. 7 days before hatching, 10.2 mm. long, left side view (embryo 6. 2). The eye is shown with dotted lines.

is not very easy to see, because it is in almost the same line as the parachordals. The hyomandibula and symplectic are beginning to be connected by faint cartilage.

Embryo 7 C 2. 6 days before hatching, 10-2 mm. long (Text-fig. 14). This stage does not differ much from the last except in so far as the hyomandibula and symplectic are more closely connected. The specimen is seen from slightly below the horizontal, which accounts for the elevated position of the auditory capsule.
**Text-fig. 14.**

*Salmo fario.*—6 days before hatching, 10.2 mm. long, left side view (embryo 7 C 2). The eye is shown with dotted lines.

**Text-fig. 15.**

*Salmo fario.* 7 days before hatching, 10.4 mm. long, left side view (embryo 6 B 1). The eye is shown with dotted lines.

Embryo 6 B 1. 7 days before hatching, 10.4 mm. long (Text-fig. 15). The notch in the hyomandibula is now definitely closed.
so as to form a foramen for the hyomandibular branch of the facial nerve. The hyomandibula and symplectic are definitely joined and fused.

Embryo 6 B 2. 7 days before hatching, 10.4 mm. long (Text-fig. 16). This embryo does not show much advance compared with the previous one as regards the neurocranium, but in the splanchnocranium the ceratobranchial of the third branchial arch has made its appearance.

Embryo 8 B 3. 5 days before hatching, 10.5 mm. long (Text-fig. 17). In this specimen again there is not much progress in the neurocranium except that the trabeculae now extend far forwards, almost to the front of the head. The ceratobranchial of the fourth branchial arch has arisen as a small elongated cartilage. In the hyoid arch the hypohyals have also arisen as independent cartilages, median to the anterior ends of the ceratohyals. The quadrate cartilage at this stage is larger than previously; it lies anterior to and parallel with the symplectic
portion of the hyomandibula. There is no trace of the pterygoid and palatine regions.

Embryo 7 B 2. 6 days before hatching, 10.7 mm. long (Text-fig. 18). The important new development in this embryo is that the auditory capsules are joined on to the anterior region of the parachordals by cartilaginous connexions, the anterior basicapsular commissures. These commissures lie behind the facial nerve, and dorsal to the head-veins (vena capitis lateralis, and secondary vein).

Embryo 8 A 1. 5 days before hatching, 10.8 mm. long (Text-fig. 19). The auditory capsules in this specimen are not only anchored on to the parachordals anteriorly by the anterior basicapsular commissures, but also farther back by the posterior basicapsular commissures, which join on to the parachordals in the region of the swelling to which attention was drawn in an earlier stage. Between the basicapsular commissures, the capsule, and the parachordal, an enclosed space is formed on each side: the basicapsular fenestra. This fenestra has been compared by Parker (1873) to the fenestra ovalis of the auditory
capsule of higher vertebrates. The posterior basicapsular commissure in *Salmo* forms behind the glossopharyngeal nerve, which therefore leaves the skull cavity through the basicapsular fenestra. This relation is apparently variable among the Teleosts, for in *Gasterosteus*, Swinnerton (1902) showed that the glossopharyngeal passed behind the posterior basicapsular and therefore with the vagus through the jugular incisure between the auditory capsule and the occipital arch. At this stage in *Salmo* the auditory capsule is beginning to rise up at the side of the auditory sacs.
Embryo 8 A 1. 5 days before hatching, 10.8 mm. long (Text-fig. 20). The visceral arches in embryos of this stage are fairly well developed. Meckel's cartilages are long and well formed; in the hyoid arch the hypohyals are present as well as the cerato-

**Text-fig. 19.**

Salmo fario. 5 days before hatching, 10.8 mm. long, dorsal view (embryo 8 A 1).

hyals, and the ceratobranchials of the first four branchial arches are present.

Embryo 11 B 2. 2 days before hatching, 11.7 mm. long (Text-fig. 21). The basicapsular commissures and the basicapsular fenestra are well seen in this embryo. The side wall of the auditory capsule is rising up, as is the occipital arch.
Text-Fig. 20.

*Salmo fario*. 5 days before hatching, 10.8 mm. long, ventral view of visceral arches (embryo 8 A 1).

Text-Fig. 21.

*Salmo fario*. 2 days before hatching, 11.7 mm. long, left side view (embryo 11 B 2).
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The stylohyal cartilage has appeared between the posterior end of the ceratohyal beneath, and that point of the hyomandibula above, where the connexion between hyomandibula and symplectic was made at an earlier stage. The quadrate and Meckel's cartilage articulate with one another, and the latter shows the retroarticular process.

It is interesting to compare the trout at this stage with an embryo of Scyllium canicula 32 mm. long (Text-fig. 22). There is a great similarity between the parachordals and the

Text-fig. 22.

Scyllium canicula. 32 mm. long, left side view.

occipital arch, indeed between the neurocrania generally. The splanchnocranium of Scyllium is somewhat different, in that the pterygoid process of the quadrate is well developed, and that in the first branchial arch the pharyngobranchial and epibranchial are present as well as the ceratobranchial. They are all independent chondrifications, as they also are in the trout, where, however, the pharyngobranchials and epibranchials do not arise until much later.

Embryo 9 A 2. 4 days before hatching, 11.4 mm. long (Text-fig. 23). No new cartilages have arisen in this specimen, but the existing ones have enlarged somewhat. The basicapsular fenestra is smaller than in previous stages, and the glossopharyngeal nerve passes through a notch. The hind part of the
auditory capsule extends farther backwards, and is overlapped by the occipital arch; the jugular incisure is therefore nearly converted into a foramen. The anterior ends of the trabeculae are expanded into plates, which slope slightly downwards and sideways.

**Text-fig. 23.**

![Diagram](image)

**Salmo fario. 4 days before hatching, 11.4 mm. long, dorsal view (embryo 9 A 2).**

Embryo 9 A 2. 4 days before hatching, 11.4 mm. long (Text-fig. 24). This view differs from the previous one of the visceral arches only in that the median copula has arisen as an independent cartilage. It is quite short, and is situated just behind the hypohyals.

Embryo 10 A 1. 3 days before hatching, 12.2 mm. long (Text-
In this embryo the side walls of the auditory capsules have grown still farther up, and the hind walls are also rising behind the posterior semicircular canals towards the occipital arches. The notches in the basicapsular fenestrae for the glossopharyngeal nerves are deeper. But the most important novelty which this embryo shows is a pair of processes which project forwards and outwards from the angle between the parachordals and the front face of the anterior basicapsular commissures. These processes pass behind the palatine branches of the facial nerves, for which reason I propose to call them the post-palatine processes. They separate the palatine branches from the hyomandibular branches of the facial nerves, and correspond to part of the post-palatine commissures which I have described elsewhere (de Beer, 1926). From the present point of view their importance lies in the fact that they are the first appearance of the lateral commissures and walls of the trigemino-facialis chambers.

Embryo 13 A 1. Just hatching, 12-3 mm. long (Text-fig. 26).
This stage is no less important than the last. In the anterior region the trabeculae have become joined, forming a trabecula communis. The glossopharyngeal nerves pass through foramina cut off from the basicapsular fenestrae. The post-palatine processes are present, and advancing as it were to meet them are processes which project inwards from the auditory capsule; these are the prootic processes.

Embryo 11 A 1. 2 days before hatching, 12 mm. long (Text-fig. 27). This stage is interesting as showing the start of the
formation of the pterygoid process of the quadrate. This region of the mandibular arch arises solely by chondrification spreading forwards from the quadrate; there is no backgrowth from the

**Text-fig. 26.**

*Salmo fario.* Hatching, 12.3 mm. long, dorsal view (embryo 13 A 1).

region of the ethmoid plate. The prootic process is visible in this figure.

Embryo 12 B 1. 1 day before hatching. 12.1 mm. long (Text-fig. 28). The pterygoid process is further developed in this embryo than in the last one; it differs from the rest of the (true) quadrate in that it is a thin plate of cartilage, whereas the
TEXT-FIG. 27.

*Salmo fario*. 2 days before hatching, 12 mm. long, left side view (embryo 11 A 1).

TEXT-FIG. 28.

*Salmo fario*. 1 day before hatching, 12.1 mm. long, left side view (embryo 12 B 1).
latter is thick and solid. The post-palatine and the prootic processes have met and joined to form the lateral commissure, which lies ventral and lateral to the vein of the head. This vein and the hyomandibular branch of the facial nerve emerge through the opening between this lateral commissure and the anterior basicapsular commissure. The side wall of the auditory capsule is rising up, but it shows a vacuity. The vertebral column has appeared at this stage, and it is curious to note that the basidorsal cartilages appear at the anterior end of the column and the basiventrals at the posterior end. At this stage (and for long after) there are no basiventrals in front.

Embryo 14 A 2. 1 day after hatching, 13 mm. long (Text-fig. 29). The trabecula communis formed by the fusion in the middle line of the trabeculae cranii is more extensive at this stage, and there is a well-formed ethmoid plate. The lateral commissure is complete, and the palatine branch of the facial nerve passes down in a notch or incisure in front of it and lateral to the trabecula. The jugular incisure is converted into a foramen, through which the vagus nerve passes, by the joining of the hind wall of the auditory capsule on to the occipital arch; the pterygoid processes of the quadrate are visible stretching forwards. At this stage also, the cartilages which will form the taeniae marginales have appeared independently (confirming Rutherford, 1909). These cartilages are probably the same as the orbital cartilages of Selachians, but they are smaller in connexion with the reduction of the side wall of the skull in Teleosts. Eventually these taeniae marginales will fuse with the auditory capsule behind, and with the lamina orbito-nasalis in front, as do the orbital cartilages of the Selachians. Unlike the latter, however, they do not connect with the subocular shelf by a pila prootica since this structure is not formed in the trout.

Embryo 14 A 2. 1 day after hatching, 13 mm. long (Text-fig. 30). The visceral arches at this stage show a number of new features. Hypobranchials have appeared as independent cartilages in the first and second branchial arches. The copula extends back to the level of the third branchial arch. Anterior to the hypohyals, the median and unpaired basihyal has ap-
peared, and although it is connected by procartilage with the copula, I think that it chondrifies separately.

Embryo 18 A 1. 5 days after hatching, 14-2 mm. long (Text-

Text-fig. 29.  

Salmo fario. 1 day after hatching, 13 mm. long, dorsal view (embryo 14 A 2).

fig. 31). At this stage the taenia marginalis has extended a little farther backwards and forwards, but it is still free. The pterygoïd process of the quadrate has also grown forwards. Typically this takes place regularly and simply from behind forwards, but
**Text-fig. 30.**

*Salmo fario.* 1 day after hatching, 13 mm. long, ventral view of visceral arches (embryo 14 A 2).

**Text-fig. 31.**

*Salmo fario.* 5 days after hatching, 14.2 mm. long, left side view (embryo 18 A 1).
occasional cases are found in which an isolated centre of chondrification appears a short distance in front of the rest of the pterygoid process, with which it soon becomes merged. Small epibranchial cartilages have appeared in the first three branchial arches, and the ceratobranchial of the fifth arch has made its belated appearance.

**Saimo irio.** 5 days after hatching, 14.2 mm. long, dorsal view (embryo 18 A 2).
Embryo 18 A 2. 5 days after hatching, 14·2 mm. long (Text-fig. 32). The taeniae marginales almost touch the anterior later corner of the auditory capsules, and anteriorly they reach nearly up to the ethmoid plate, but of course at a higher level. The basicapsular fenestra has become divided into two, as the floor of the auditory capsule becomes more completely developed. The sides of the auditory capsule are beginning to grow in over

**Text-fig. 33.**

*Salmo fario*. 7 days after hatching, 15·5 mm. long, left side view (embryo 20 A 2).

the auditory sac, forming a roof. The septa, which pass through the semicircular canals, are beginning to develop. That for the posterior canal is seen at this stage, running from the side wall of the capsule backwards and inwards to the occipital arch. The roof over the posterior canal remains procartilaginous for some time.

Embryo 20 A 2. 7 days after hatching, 15·5 mm. long (Text-fig. 33). From the hinder part of each side of the ethmoid plate a process rises up towards the taenia marginalis; this is the lamina orbito-nasalis (antorbital process of Gaupp, 1906; par-
Salmo fario. 7 days after hatching, 16 mm. long, dorsal view (embryo 20 A 1).
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ethmoid cornu of Swinnerton in *Gasterosteus*, 1902; ectethmoid process of Kindred in *Syngnathus*, 1921). The taenia marginalis has fused with the auditory capsule posteriorly.

Embryo 20 A 1. 7 days after hatching, 16 mm. long (Text-fig. 34). The basicapsular fenestra is still more reduced at this stage; and the roof of the auditory capsule has extended over

Embryo 21 B. 8 days after hatching, 16 mm. long (Text-fig. 35). The lamina orbito-nasalis has almost met the anterior end of the taenia marginalis. The pterygoid process now extends well up to the ethmoid plate. In this specimen the most anterior region of the pterygoid process appears to be chondrifying separately. I am not, however, of the opinion that this is
of much importance, although it might possibly have a bearing on the future double articulation of the pterygoid process with the ethmoid plate. At all events this chondrification is connected with the rest of the pterygoid process by procartilage.

Embryo 25 B. 12 days after hatching (Text-fig. 36). This embryo is seen from in front, and shows the state of affairs in the ethmoid region of the skull very plainly. The internasal septum rises up in the centre of the ethmoid plate, and on each side

Text-fig. 36.

Salmo fario. 12 days after hatching, front view (embryo 25 B).

are the laminae orbito-nasales. The taeniae marginales converge as they come forwards, and each bifurcates to form a median process pointing to the internasal septum, and a lateral process leading to the lamina orbito-nasalis.

Embryo 23 A. 10 days after hatching, 16·3 mm. long (Text-fig. 37). The lamina orbito-nasalis has joined on to the taenia marginalis, and the internasal septum has all but fused with the median processes of the taeniae marginales. The anterior end of the pterygoid process bears what appear to be the two future articular heads (rostro-palatine and ethmo-palatine).

Embryo 22 A 1. 9 days after hatching, 16·5 mm. long (Text-fig. 38). This embryo is not very dissimilar from the last. The epiphysial bar has formed between the taeniae marginales, and,
on one side, the incisure for the palatine nerve has been converted into a foramen. Sections show that this enclosure takes place by a growth of cartilage from the lateral commissure inwards towards the edge of the subocular shelf. This cartilage probably represents the basitrabecular process. Posteriorly a very small basidorsal cartilage has appeared just behind the occipital arch. It seems to belong to a vertebral element in process of reduction.

**Text-fig. 37.**

*Salmo fario.* 10 days after hatching, 16.3 mm. long, left side view of anterior region of skull (embryo 23 A).

Embryo 24 A 1. 11 days after hatching, 16.5 mm. long (Text fig. 39). The front of the ethmoid plate has grown out into a rostrum, and the nasal septum is now completely formed. On each side of it is an opening, the orbito-nasal fissure, enclosed at the side by the lamina orbita-nasalis. The rostro-palatine and ethmo-palatine articulations are indicated. The hypobranchials of the fourth branchial arch have appeared. The auditory capsule is drawn showing the channels for the semicircular canals and their septa as seen by transparency.

Embryo 28. 15 days after hatching (Text-fig. 40). This
Salmo fario. 9 days after hatching, 16.5 mm. long, dorsal view (embryo 22 A 1).
TEXT-FIG. 39.

Salmo fario. 11 days after hatching, 16.5 mm. long, left side view (embryo 24 A 1).
embryo is seen from in front, and shows the relations of the internasal septum to the laminae orbito-nasales. Dorsal to the orbito-nasal fissure is a small foramen through which a branch of the ophthalmic nerve passes.

Embryo 27. 14 days after hatching, 17.5 mm. long (Text-fig. 41). The copula has segmented into two pieces, of which the anterior is related to the first three branchial arches, and the posterior to the last two. The fifth arch has no hypobranchial. Pharyngobranchial cartilages are present in the first two branchial arches, and epibranchials in the first three. In some cases I have observed that the fourth hypobranchial arises in cartilaginous continuity with the ceratobranchial. In no case, however, does the ceratobranchial break up to form the other elements of the branchial arch. The hypohyals are notched in front, and lodge the afferent hyoidean arteries.

Text-fig. 42 is a dorsal view of a model reconstructed from an embryo in a slightly more advanced stage of development than the preceding one. The roof of the skull is represented by the tectum in front between the taeniae marginales, and behind by the tectum synoticum. The basicapsular fenestrae are almost closed over, but the cartilage in this region remains very thin. The prootic bridge has developed between the parachordals, just in front of the tip of the notochord, and enclosing a basicranial fenestra. The median side of the anterior regions of the para-

Salmo fario. 15 days after hatching, front view (embryo 28).
chordals and trabeculae just in front of the prootic bridge are depressed, and lie at a lower level than the rest of the basal plate. This depression contributes to the formation of the myodome.

TEXT-FIG. 41.

*Salmo fario*. 14 days after hatching, 17.5 mm. long, dorsal view of visceral arches (embryo 27).

and as the palatine foramina pierce that part of the cartilage which becomes depressed, the palatine nerves find themselves traversing the myodome. The prootic bridge forms part of the
Salmo sp. Circ. 14 mm. Dorsal view of a wax-model reconstruction.
roof of the myodome. It will be noticed that there is only one foramen for the passage of both the head-vein and the hyo-mandibular branch of the facial nerve. Gaupp found two separate foramina in Salmo salar (1906), and Winslow found them also in Salmo fontinalis (1896). I have been unable to find these foramina separate in Salmo fario. The pterygo-quadrate bears small basal and otic processes.

DISCUSSION OF RESULTS.

The Parachordal Cartilages.

In spite of the large number of preparations and sections examined and studied, in no case was the parachordal observed to arise as separate anterior and posterior cartilages, as Stöhr describes (1882). I am inclined to think, therefore, that the separate chondrification of the anterior region of the parachordal in Salmo is not typical, if it occurs. Stöhr worked on Salmo salar and Salmo trutta, and it is of course possible that in these species this method of origin may be usual. Against this, however, is the fact that Tichomiroff (1885), also working on Salmo salar, did not find separate anterior parachordal cartilages. Further, Professor van Wijhe has kindly informed me that neither he nor his students were able to find them either. Since it is abundantly clear that these cartilages, even if they were separate, could not be pole cartilages, for they are situated too far posteriorly and enter into relations with the auditory capsule, the matter is not one of great importance. It has already been seen that exceptions in Salmo fario show the joined appearance of trabeculae and parachordal from the first, instead of separate chondrification; but these cases cannot be considered to be of any significance. Comparable variations in method of appearance were observed by Swinnerton (1902) in Gasterosteus, in which also he observed separate anterior and posterior chondrifications in the parachordals. In Amia also, according to Pehrson (1922), separate chondrifications arise in the parachordals. In Sebastes and Cyclopterus, on the other hand, Uhlmann (1921) found that the parachordal chondrified in one piece.
My sections of Salmo do, however, show a dense region of procartilage at the point where Stöhr’s anterior parachordals should be, and it is possible either that in exceptional cases this region may chondrify separately, or that when using stains which are not as specific for cartilage as those of van Wijhe’s method, these regions may be mistaken for cartilage. In this connexion Stöhr (1882) states that he distinguishes cartilage from procartilage as soon as the cells are visibly differentiated from the surrounding cells, and as soon as an intercellular matrix has appeared.

Relations to the Cartilages of the Nerves, Blood-vessels, and Muscles.

The internal carotid arteries enter the cranial cavity through the hypophysial fenestra, but just before doing so, they come into contact with the efferent pseudobranchial arteries (mandibular vessels). The degree of connexion between the carotid and the efferent pseudobranchial seems to vary in different specimens. The continuation of the efferent pseudobranchial is the arteria ophthalmica magna, which leaves the skull passing dorsal to the trabecula. The pseudobranch is situated ventromedial to the small basal process of the pterygo-quadrate. The afferent pseudobranchial vessel runs laterally beneath the otic process, and in front of the hyomandibula. It then leads down along the hyoid arch and lies on the ventro-lateral face of the ceratohyal, passing through a notch in the hypohyal to join its fellow from the other side and form the ventral aorta.

The orbital artery (external carotid of Allis, 1912) leaves the internal carotid beneath the auditory capsule, and running upwards, enters the trigemino-facialis chamber by its posterior opening. It enters median to the head-vein, but within the chamber it passes upwards over the latter and comes to lie on its outer side when it emerges from the anterior opening of the trigemino-facialis chamber.

Farther forward, the internal carotid gives off a small artery which passes through the palatine foramen, and so enters the myodome. It runs morphologically median and anterior to the
Text-fig. 43.

Salmo sp. Dorsal view of the model shown in Text-fig. 42, with the chief blood-vessels, nerves, and muscles inserted. For the sake of clarity the buccal and ophthalmic nerves are omitted.
palatine nerve. This artery runs forward over that portion of the lateral commissure that corresponds to the basitrabecular process, and continues its way through the orbit. It passes ventral to the ophthalmica magna, and to all the eye-muscles except the inferior oblique. It is accompanied most of the way by the branch of the oculomotor that innervates the inferior oblique, and which passes down from the ciliary ganglion lateral to it (artery). At the anterior end of the orbit this artery passes through the orbito-nasal fissure into the nasal region. In Text-figs. 43 and 44 this artery is figured and called the orbito-nasal artery. It is important to note that an artery with exactly identical relations exists in Lepidosteus (18 mm. and 25 mm. specimens). This artery, which Allis (1909) also called the external carotid, I called the orbital artery (de Beer, 1926). At the same time, the embryos of Lepidosteus which I have studied have a very small artery which pursues the same course as the orbital artery of Salmo. It is unprofitable to attempt to make absolute homologies between the orbital arteries of these fish, especially, as in Amia, the artery which Allis (1900) called the
external carotid and which I consequently also called the orbital artery, enters the trigemino-facialis chamber through a small foramen of its own and lies lateral to the palatine nerve, instead of median to it as in Lepidosteus. (It may be noticed, by the way, that the orbital artery in Selachians also passes morphologically median and anterior to the palatine nerve.) However, the perfect similarity in relations between the orbito-nasal artery of Salmo and the so-called orbital artery of Lepidosteus suggests that they are homologous, and that the structures to which they bear these constant relations are respectively homologous also. This matter will be considered again below in connexion with the lateral commissure, and the ethmoid region of the skull.

The relations of the remaining structures are sufficiently clearly shown in Text-figs. 43 and 44, and do not require further description.

The Ethmoid Region.

It is well known that in Salmo, as in so many other Teleosts, the olfactory nerves pass for a certain distance through the orbit on the way to the nasal capsules. They therefore have to pass through two foramina: foramen olfactorium evheens (Gaupp, 1906) from the cranial cavity into the orbit, and foramen olfactorium advehens from the orbit to the nasal capsule. In order to explain this remarkable state of affairs, Sagemehl (1885) imagined that there had been a progressive fenestration and perforation of the wall of the cranial cavity in the anterior region of the orbit, and that by this means the olfactory nerve was able to, as it were, slip out into the orbit. He observed in the development of Salmo that the lobus olfactorius always remained close to the brain, and that no tractus was developed, such as there is in Gadus (see Goodrich, 1909). In other words, the 'Teleost' type arises direct from the 'Cyclostome' type.

Gaupp (1906) regarded it as more probable that a fenestration had taken place not in the wall of the cranial cavity, but in the side of an olfactory canal, such as is present in Amia (see Allis, 1897). Such is also the view of Norman (1926). Dietz (1921) was more concerned with the conditions in the Gadidae.
than with the origin of the 'Teleost' condition, to use Sagemehl's term. It appears to me that neither Sagemehl's nor Gaupp's theories are entirely satisfactory to account for the

Text-fig. 45.

*Lepidosteus osseus*. Diagrammatic reconstruction of the relations of the ethmoid region of an embryo 18 mm. long, seen from the left side.

Text-fig. 46.

*Salmo sp.* Diagrammatic reconstruction of the relations of the ethmoid region of an embryo 14 mm. long, seen from the left side.

passage of the olfactory nerve through the orbit, and that a simpler explanation is available. Turning to *Acipenser* (Text-fig. 48), there is a plate of cartilage which separates the orbit from the nasal capsule. This cartilage, or lamina orbitonasalis, is pierced by a small foramen through which blood-
vessels make their way from the orbit to the nasal capsule. The lamina orbito-nasalis appears to correspond with the similarly named structure in Selachians (see van Wijhe, 1922), where it arises as a lateral process from the trabecula and meets the orbital cartilage. The oblique eye-muscles are attached to the skull-wall posterior to the lamina orbito-nasalis. In *Lepidosteus* (18 mm., Text-figs. 45 and 49) there is a small lamina orbito-nasalis called by Veit (1911) a process on the orbito-nasal plate. The front edge of this structure is level with the olfactory foramen. It reaches upwards and touches the side-wall of the cranial cavity, leaving a passage through which the orbit communicates with the nasal capsule, and through which the orbito-nasal artery (described above) passes. The oblique eye-muscles are attached to the side of the skull-wall posterior to the lamina orbito-nasalis.

In *Amia* the lamina orbito-nasalis is also present, and is called cornu parahmiodale by Pehrson (1922). Its anterior edge is anterior to the olfactory foramen, and as it also leaves a passage between itself and the side-wall of the skull through which blood-vessels run from the orbit to the nasal capsule, the
olfactory nerve finds itself in a canal. This condition is easily derived from that in Lepidosteus by a relative anterior shifting of the position of the lamina orbito-nasalis. The com-

Text-figs. 48-51.

Diagrammatic representations of the relations of the olfactory nerves to the surrounding structures in Text-fig. 48, Acipenser; Text-fig. 49, Lepidosteus; Text-fig. 50, Amia; Text-fig. 51, Salmo. The crosses indicate corresponding points in the different types.

munication of the canal with the orbit is not a new fenestration, but the orbito-nasal fissure, through which the blood-vessels pass, and which is present in Lepidosteus although that fish has no olfactory 'canal' at all. It is important to note,
however, that in Amia (Text-fig. 50) the oblique eye-muscles have made their way into the orbito-nasal fissure and olfactory canal, which is not a portion of the cranial cavity. A continuation of the processes which have converted the conditions of Lepidosteus into such as are shown in Amia, leads to Salmo (Text-figs. 46, 47, and 51). A further relative forward movement of the lamina orbito-nasalis causes the olfactory foramen to open behind it; and as the lamina orbito-nasalis marks the anterior limit of the orbit, the olfactory foramen opens into the orbit. This is the foramen olfactorium evehens of Gaupp. His foramen olfactorium advehens is really part of the orbito-nasal fissure, and it is traversed also by the orbito-nasal artery as described above. The oblique eye-muscles reach forward median to the lamina orbito-nasalis and are attached to the internasal septum which, as development proceeds, is hollowed out to form the anterior eye-muscle canal. In earlier stages the only portions of the anterior region of the true brain-case which are chondrified are the taeniae marginales, or orbital cartilages. The lamina orbito-nasalis is not part of the true brain-case (Text-fig. 46). The remainder of the brain-case chondrifies later (Text-fig. 47, Salmo fario, 30 mm.).

The relations of the olfactory nerve can thus be explained without postulating any perforation, but by a relative forward movement of the lamina orbito-nasalis with regard to the olfactory foramen in fish which already had an orbito-nasal fissure. It becomes interesting to inquire whether this relative movement has concerned the lamina orbito-nasalis or the site of the olfactory foramen or both. This matter is not easy to decide in view of the fact that no point can be regarded as fixed. I have, however, obtained the following measurements of certain lengths in corresponding stages of Lepidosteus, Amia, and Salmo. With regard to Lepidosteus, care was taken to select a stage before the elongation of the skull takes place. These results are tabulated below, and Text-fig. 52 is a diagram drawn to scale of these relations.
Distance between optic nerve and olfactory foramen . . . . 0·735 mm. 1·89 mm. 1·32 mm.
Distance between olfactory foramen and front edge of lamina orbito-nasalis . . . . 0 mm. 0·27 mm. 0·54 mm.
Length from front to rear of lamina orbito-nasalis . . . . 0·09 mm. 0·36 mm. 0·22 mm.
Length of inferior oblique muscle . . . . 0·4 mm. 1·5 mm. 1·2 mm.

No value is to be attached to these figures by themselves; it is only when they are regarded as proportions and compared that an interesting fact appears. In Text-fig. 52 the distance between the optic nerve and the olfactory foramen is taken as constant, and it is obvious how little change is required to modify one type into another. This would be equally apparent whatever dimension was taken as constant. The diagram also shows the intermediate position of Amia. Of the same three forms Amia is also intermediate as regards the posterior myodome; and as the modifications of the ethmoid region which are being considered here are also associated with eye-muscles, it is just possible that the two sets of facts may not be entirely unconnected.

It would have been possible to construct Text-fig. 52, taking the distance between the lamina orbito-nasalis and the optic nerve as constant, and this would have shown the progressive withdrawal towards the tail of the olfactory foramen, instead of the progressive advance of the lamina orbito-nasalis.

It is difficult to decide which of these possibilities has produced the conditions in Salmo, but a consideration of the oblique eye-muscles suggests that the forward movement of the lamina orbito-nasalis is the more probable, although it need not absolutely exclude the other. The oblique eye-muscles are relatively longer in Amia than in Lepidosteus, and still longer in Salmo than in Amia. There is a good reason, therefore, why the lamina orbito-nasalis should have moved forwards, and allowed the muscles to reach the internasal septum.
It is to be concluded, then, that the foramen olfactorium evehens of Salmo represents the original olfactory foramen. Consequently that portion of the interorbital septum which lies in front of the foramen (olfactorium evehens) of Salmo corresponds to some part of the internasal septum of other forms. It has been thrown into the orbit by the expansion of the latter.

The Lateral Commissure.

Text-fig. 52.

Diagram illustrating the relations of the olfactory nerves, lamina orbito-nasalis, and orbit, in Lepidosteus, Amia, and Salmo; drawn to scale and plotted so as to make the distance between the optic nerve and the olfactory foramen equal.

It has been shown that the lateral commissure in Salmo is formed from three elements, and in the following order:

1. Post-palatine process.
2. Prootic process.
3. Cartilage corresponding in position to a basitrabecular process.

In Amia the lateral commissure is formed of the same elements, but they appear in precisely the reverse order: 3, 2, 1. Further,
while there is a proper basitrbecular process in \textit{Amia} formed as an extension to the side of the subocular shelf, in \textit{Salmo} the cartilage which corresponds to it in position grows towards the subocular shelf from the joined post-palatine and prootic processes. In \textit{Lepidosteus}, according to Veit (1911), the lateral commissure is formed from 1, post-palatine process ('Knorpelspange, welche von dem Parachordale... zur Ventralfläche der Ohrkapsel zieht'); he does not mention a prootic process, but it is possible that a small one is present. The basitrbecular process is properly developed.

In spite of these variations in the methods of formation, there can be little doubt that the trigemino-facialis chambers, and therefore the lateral commissures also, of these three fish are homologous. The relations of the palatine nerve and of the orbital artery of \textit{Lepidosteus} to its undoubted basitrbecular process suggest that the corresponding region in \textit{Salmo}, which bears identical relations to the palatine nerve and to the orbito-nasal artery, represents the basitrbecular process in spite of the difference in method of origin.

These investigations therefore support the conclusions to which I previously arrived, to the effect that the lateral commissure is a connexion between the subocular shelf and the auditory capsule; it may grow out from the subocular shelf in front of or behind the palatine nerve, or both in front of and behind it, and the auditory capsule may also take part in its formation. It contains the representatives of the basitrbecular process and of the post-palatine commissure. Its development in \textit{Lepidosteus}, \textit{Amia}, and \textit{Salmo} lends no support to Allis's view that it corresponds to the otic process (Allis, 1914); indeed, this view is impossible to reconcile with the presence of a rudimentary otic process on the pterygo-quadrate of \textit{Salmo} and of \textit{Amia}.

\textbf{Summary.}

1. The parachordal of \textit{Salmo fario} was not observed to chondrify in two separate portions, anterior and posterior.
2. No separate pole cartilages were found.
3. The first part of the auditory capsule to arise is in the region where the hyomandibula will become attached to it.

4. The hyomandibula, symplectic, and ceratohyal arise as separate cartilages.

5. The hypohyals, basihyal, and copula arise as separate cartilages.

6. The ceratobranchials, hypobranchials, epibranchials, and pharyngobranchials (at least the anterior) arise as separate cartilages.

7. The lateral commissure is formed from the post-palatine process, the prootic process, and cartilage representing the basitabecular process.

8. The taenia marginalis (or orbital cartilage) arises separately.

9. Rudimentary basal and otic processes are carried on the pterygo-quadrate.

10. The olfactory nerve comes to traverse the orbit as a result of the relative forward displacement of the lamina orbitonasalis.

LIST OF LITERATURE CITED.


—— (1909).—“The cranial anatomy of the mail-checked fishes”, ‘Zool. logica’, 22.


—— (1914).—“The pituitary fossa and trigemino-facialis chamber in Ceratodus forsteri”, ibid., 46, p. 625.


Gaupp, E. (1906).—"Die Entwicklung des Kopfskelettes", in Hertwig's 'Handbuch der vergl. und exper. Entwick. der Wirb.'


Parker, W. K. (1873).—"On the structure and development of the skull in the Salmon", ibid., 163, p. 95.


