IX. *The Development of the Chondrocranium of the Eel* (Anguilla vulgaris), *with Observations on the Comparative Morphology and Development of the Chondrocranium in Bony Fishes.*

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(*Communicated by Prof.* E. W. MACBRIDE, *F.R.S.*)

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INTRODUCTION.

THIS paper furnishes descriptions of certain stages in the development of the chondrocranium of the Common Eel (*Anguilla vulgaris*, Turton), and, in addition, provides a comparative account of the chondrocranial development in Bony Fishes, and particularly in the Teleosts. Since the publication of HERTWIG'S* treatise on comparative vertebrate embryology in 1906, in which the section dealing with the cranial skeleton was written by the late Prof. GAUPP, no adequate comparative study of the fish chondrocranium has been undertaken; in view of the fact that our knowledge of the subject has been considerably augmented in recent years, an endeavour to supply this deficiency

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* HERTWIG, O., 'Handbuch d. vergl. u. experiment. Entwick. d. Wirbeltiere,' Jena, 1906.

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seemed desirable. Owing to the limited time at my disposal, and the probability of the investigation being prolonged indefinitely, this comparative investigation is far from complete.

In planning out the paper it was found convenient first to describe the development of the chondrocranium in *Anguilla*, and to postpone the discussion and interpretation of the results to the latter part of the paper. The stages here described extend to the metamorphosis of the larval *Leptocephalus*, at which time the chondrocranium has attained its maximum development. Certain observations on the later stages are recorded, in so far as they affect the interpretation or ultimate fate of the cartilaginous parts of the skull; it is hoped to describe these stages in greater detail, and to deal with the changes which lead to the formation of the adult skull in a subsequent paper.

The second part of this paper is devoted to a comparison of the more important features in the chondrocranial development in Ganoids* and Teleosts. Observations on the Selachians and Dipnoans are included only in connection with questions relating to the homologies of cartilages, etc., but references to the more important papers dealing with the chondrocranium in both these groups of fishes are included in the list of references at the end of this paper. The results included in this comparative section are based partly on the published accounts of other investigators, and partly on the study of preparations of a number of embryo and larval fishes in my possession.

The material, on which the description of the chondrocranium of *Anguilla* is based, was handed to me for investigation by Dr. JOHANNES SCHMIDT, at whose suggestion the work was undertaken; for his generosity in providing me with a large series of *Leptocephalus* larvæ I wish to tender my sincere thanks. I am indebted to Prof. H. H. SWINNERTON for preparations of *Gasterosteus* and many other larval fishes; to Mr. F. R. WELLS for the loan of his preparations of larval *Clupea*†; to Mr. N. A. MACKINTOSH for the loan of his sections of larval *Sebastes*; to Prof. A. MEEK for sections of larval *Galaxias*; and to Mr. B. STORROW for specimens of young *Clupea* and *Zoarces*: to all these gentlemen my thanks are due and are gratefully tendered.

The investigation was commenced early in 1920 at the Huxley Research Laboratory of the Imperial College of Science and Technology, under the supervision of Prof. E. W. MACBRIDE, F.R.S. Since my appointment to the Natural History Museum the work has been continued at irregular intervals. I wish to take this opportunity of expressing my gratitude to Prof. MACBRIDE, to Mr. C. TATE REGAN, M.A., F.R.S., and to Dr. H. GRAHAM CANNON, for frequent advice and many helpful suggestions given during the course of the work.

The number of illustrations accompanying the first part of this paper is somewhat

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* The term "Ganoids" is here used in a very general sense, and includes the Acipenseridæ, Polyodontidæ, Polypteridæ, Amiidæ, and Lepidosteidæ.

† Soon after this work had been commenced I suggested to Prof. MACBRIDE that a study of the Clupeid chondrocranium might prove to be of interest; such a study has been carried out by Mr. F. R. WELLS in Prof. MacBride's laboratory; his results were published in 1923.

large, but in order to make certain observations clearly intelligible it has been found necessary to figure some critical sections in addition to models of the whole chondrocranium. The figures have been made somewhat severely diagrammatic, and no attempt has been made to reproduce histological details.

Literature.

The only published descriptions of the chondrocranium of *Anguilla* appear to be those of Facciola (1897, 1901, 1903) and Torlitz (1922). The former has dealt with the general anatomy of *Leptocephalus*, and has briefly described, but has not figured the chondrocranium; his nomenclature makes it difficult to follow his description. Torlitz describes and figures the chondrocranium of a larva 66 mm. long, and has also studied the cranium of the Elver (Glasaal) and adult Eel.

The investigation of the ontogeny of the chondrocranium of a particular fish stage by stage has been undertaken by comparatively few workers. The more important of these papers, in which (generally) three or more stages are described, are included in the following list, the fishes investigated being arranged in systematic order.

I.—SELACHII.

Squalus [*Acanthias*].—Sewertzoff (1897, 1899); Wijhe (1905, 1922).
Scyliorhinus [*Scyllium*].—Parker (1878); Goodrich (1918).
Pristiurus.—Sewertzoff (1897, 1899).
Heterodontus [*Cestracion*].—De Beer (1924a).
Raia.—Parker (1878).
Callorhynchus.—Schauinsland (1903).

II.—PISCES.

Acipenser.—Parker (1882a).
Polypterus.—Budgett (1907); Kerr (1907); Lehn (1918).
Amia.—Pehrson (1922).
Lepidosteus.—Parker (1882b); Veit (1907, 1911).
Clupea.—Wells (1923).
Salmo.—Parker (1873); Stöhr (1882); Gaupp (1906).
Gymnarchus.—Assheton (1907).
Amiurus.—Kindred (1919).
Exocoetus.—Lasdin (1913).
Syngnathus.—McMurrich (1883); Kindred (1921, 1924).
Gasterosteus.—Swinnerton (1902).
Sebastes.—Mackintosh (1923).
Cyclopterus.—Uhlmann (1921).
Pleuronectes, *Solea*.—Berrill (1925).
Protopterus, *Lepidosiren*.—Agar (1908).
Ceratodus.—Krawetz (1911).

In addition to the above, a number of papers have been published either dealing with one or two isolated stages in the ontogeny of the chondrocranium of certain fishes, or concerned merely with the development of a specific part of the same. A list of the more important of these papers follows, in which, for convenience, the authors' names are placed in alphabetical order, and opposite each name is placed the particular fish or fishes studied by that author.

ALLIS (1917).—*Chimæra.*
,, (1920).—*Lepidosteus.*
BOKER (1913).—*Salmo.*
DE BEER (1924b).—*Scyliorhinus, Heterodontus, Amia, Salmo, Cottus, Ceratodus.*
DOHRN (1884).—Selachii.
FÜRBRINGER (1903).—Selachii.
GANIN (1880).—*Rhodeus, Gasterosteus.*
HOFFMANN (1896).—Selachii.
LASDIN (1916).—*Symbranchus.*
NUSBAUM (1908).—*Cyprinus.*
POLLARD (1895a).—Siluroidea.
,, (1895b).—*Polypterus, Silurus, Gobius, Ceratodus.*
POUCHET (1878).—*Clupea, Syngnathus, Labrus Atherina, Gobius.*
RUTHERFORD (1909).—*Salmo.*
RYDER (1881a).—*Cybium.*
,, (1881b).—*Hippocampus.*
,, (1886).—*Gambusia.*
,, (1887).—*Clupea, Ictalurus.*
SCHLEIP (1904).—*Salmo.*
SCHREINER (1902).—*Amia, Lepidosteus.*
SEWERTZOFF (1902).—*Ceratodus.*
,, (1923).—*Squalus, Acipenser.*
WALTHER (1883).—*Esox.*
WIJHE (1882).—*Amia, Lepidosteus, Ceratodus.*
WILLIAMS (1902).—*Pseudopleuronectes.*
WILLCOX (1899).—*Salmo.*
WINSLOW (1898).—*Polypterus, Salmo, Protopterus.*
ZANICHELLI (1909).—*Salmo.*

MATERIAL AND METHODS.

The material of *Anguilla vulgaris* studied consisted of 15 larvæ (*Leptocephalus brevirostris*) prior to the metamorphosis, ranging in length from 5 mm. to 78 mm.; 3 larvæ representing stages during the metamorphosis, of 71 mm., 70 mm., and 64 mm.

respectively; and 3 elvers.* Only the præmetamorphosis larvæ are dealt with in detail in this paper, and these have been grouped for convenience into three stages. Expressed in tabular form, the particulars of this material are set out below:—

Stage.	Ref. No.	Total length of specimen.	Manner in which studied.
		mm.	
I.	A.†	5	T.S.
,,	B.	6	W.M.
,,	C.	7	T.S.
,,	D.	8	W.M.
,,	E.	9	T.S.
II.	F.†	11	,,
,,	G.	13	,,
,,	H.	17	,,
,,	I.	20	L.S.
III.	J.	24	T.S.
,,	K.	30	W.M.
,,	L.†	31	T.S.
,,	M.	40	,,
,,	N.	45	,,
,,	O.	78	,,
	P.‡	71	T.S.
	Q.‡	70	,,
	R.‡	64	,,
	S.	Elvers.	,,
	T.		,,
	U.		L.S.
	V.	Adult.	Spirit specimen and dried skulls.

L.S. = serial longitudinal sections; T.S. = serial transverse sections; W.M. = whole mount.

All the *Leptocephalus* material had been preserved in formalin, and the state of preservation was generally fairly satisfactory, although that of the smaller examples was poor. The majority of the specimens were studied by means of serial transverse sections, but series of longitudinal sections and whole mounts were also employed. Each larva was stained in bulk with borax carmine, and was examined and drawn before embedding in paraffin wax. Sections from 6μ (for the smaller examples) to 15μ thick were cut, and stained with hæmalum and picronigrosin, MALLORY's triple stain, EHRLICH's hæmatoxylin and orange g., and with EHRLICH's hæmatoxylin and picronigrosin; the last method was found to give the best results. Reconstructions of selected

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* I am indebted to Dr. J. W. WILLIS BUND for a number of elvers collected in the River Severn, and preserved in Bouin's fluid.

† Reconstructions in wax were made of these specimens.

‡ Metamorphosis stages.

specimens were made in wax, using a modification of the BORN method as described by me elsewhere.* As a control for these wax models, further reconstructions were made on squared paper, using the method suggested by WELLS (1923, p. 1214). Attempts were made to prepare whole mounts of the heads of larvæ after staining with methylene blue, as suggesed by WIJHE,† but the results did not prove satisfactory.

In connection with the study of the comparative morphology of the chondrocranium, I have studied preparations of embryos or larvæ of the following Neopterygian fishes :—*Amia, Clupea, Galaxias, Salmo, Gymnarchus,*‡ *Siphonostoma, Haplochilus, Gadus, Motella, Gobius, Callionymus, Blennius, Zoarces, Sebastes, Cyclopterus, Gasterosteus* and *Pleuronectes*. In addition, serial sections of certain embryo Selachians and of larval *Polypterus* and Dipnoi have been examined.

DEVELOPMENT OF THE CHONDROCRANIUM IN *Anguilla vulgaris*.

Stage I.

The description of this stage is based on a reconstruction made from a larva of 5 mm.; serial sections and entire preparations of larvæ of 6 to 9 mm. were also studied.

Neurocranium.—The ethmoid region is already well developed, and consists of a narrow ethmoid plate (figs. 1, 4, *e.p.*), which in its broadest part is only twice the width of the trabecula communis. The ethmoid plate is continuous dorsally, with a massive mesethmoid cartilage or ethmoid septum (figs. 1, 2 and 4, *m. eth.*), the combined cartilages being continued anteriorly as a short rostrum (figs. 1, 2, and 3, *r*), which is bluntly pointed and shows no trace of anterior angles or præ-ethmoid cornua. No independent rostral cartilage is developed at any stage. Opposite the middle of the nasal organs the median part of the mesethmoid cartilage becomes much thinner, and a little farther back disappears (fig. 4); the thick upper portion is continued posteriorly as a solid mass of cartilage, which soon divides to form the paired supraorbital bars (fig. 4, *m. eth.*).

The anterior part of the membranous interorbital septum stretches from this upper posterior portion of the mesethmoid cartilage to the ethmoid plate (fig. 4, *i. sp.*), and the oblique eye-muscles appear to have their attachment in the surrounding connective tissue (*i.o.m.*). The nasal organs lie on either side of the mesethmoid, but are otherwise entirely unprotected by cartilage (figs. 3, 4, *n.o.*); the olfactory nerves appear to run freely across the anterior corners of the orbits before turning dorsally in order to enter the brain cavity. The latter ends blindly in the fissure, where the supraorbital bars diverge from the posterior end of the mesethmoid cartilage. The brain already occupies a posterior position with regard to the ethmoid region of the neurocranium, no part of it being situated either on or above the ethmoid plate.

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* 'Journ. R. Micros. Soc.,' 1923, pp. 37–56, 8 figs.

† 'Proc. Kon. Akad. Wet.,' Amsterdam, 1902.

‡ Through the courtesy of Prof. J. GRAHAM KERR, I have re-examined certain of the preparations studied by ASSHETON (1907), which are now preserved in the Zoological Department, Glasgow University.

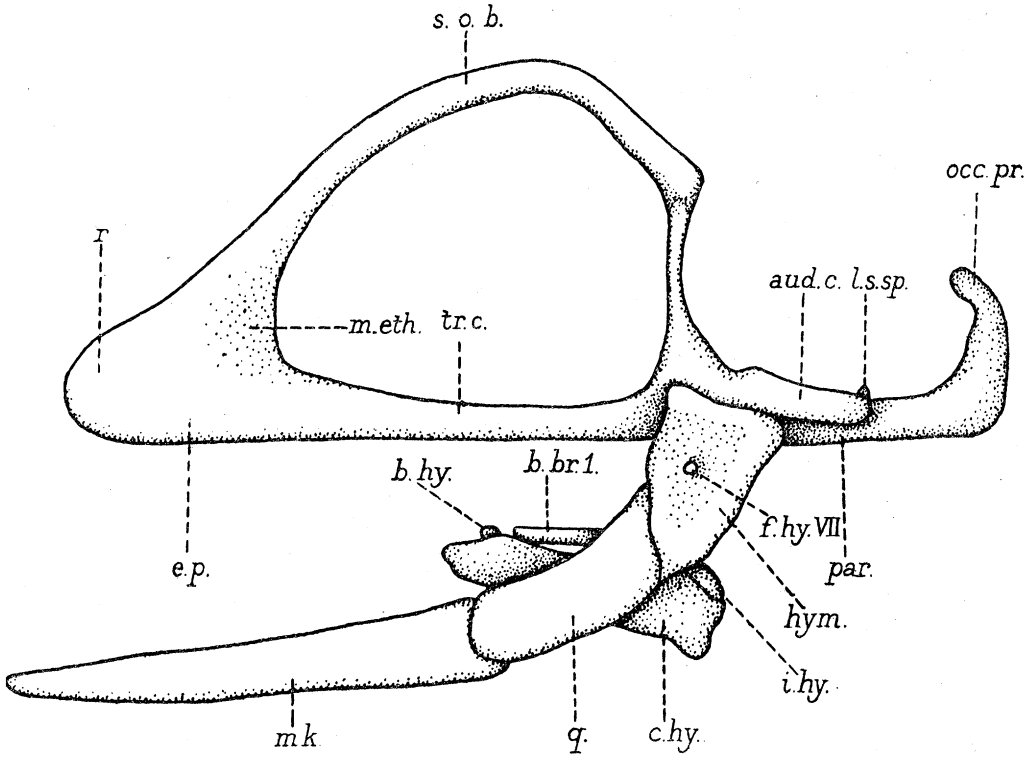

FIG. 1.—Lateral view of the chondrocranium of a 5-mm. larva of *Anguilla vulgaris*, × 157. The branchial cartilages are omitted.

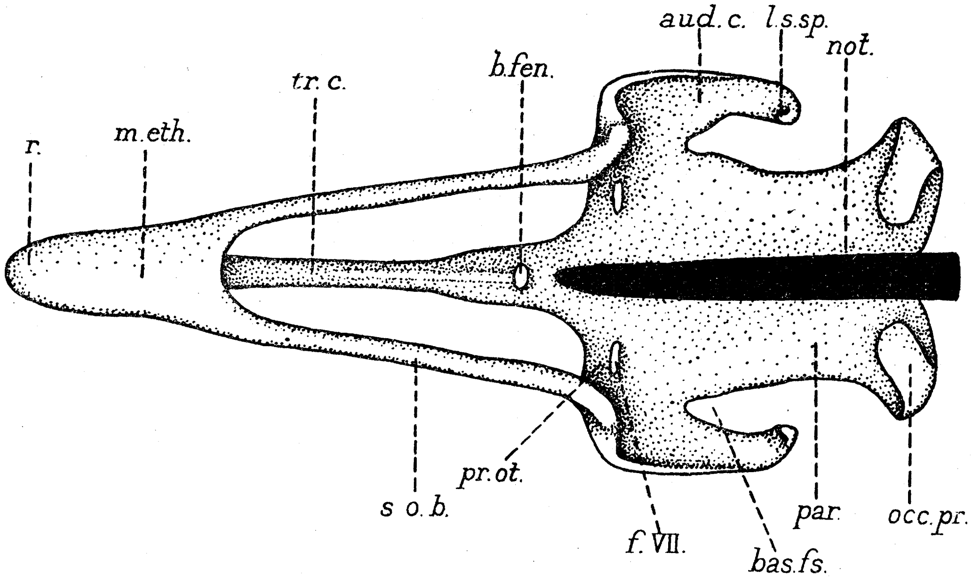

FIG. 2.—Dorsal view of the neurocranium of the same larva, × 157.
Drawings made from a wax model 420 times the actual size of the chondrocranium.

(See key to lettering at end of paper.)

The trabeculæ are completely fused for the greater part of their length to form a median trabecula communis (figs. 1, 2, *tr. c.*), the chondrocranium being, thus, of the "tropibasic"* type typical of most teleostean fishes. This cartilaginous bar is somewhat narrowed between the large eyes, and is continuous anteriorly with the ethmoid plate. It is sharply keeled above and broadly rounded below, so that the bar appears roughly pear-shaped in transverse section. Only in the region of the basicranial fenestra does it show any trace of its double character (fig. 5, *tr.*). The fenestra itself (figs. 2, 5, *b. fen.*) is extremely small, and is situated immediately in front of the hypophysis, which lies at some distance above the base of the chondrocranium. Behind the fenestra the trabecular cartilages are again indistinguishably fused, and more posteriorly they pass imperceptibly into the anterior parachordals, no line of division between them being apparent even at this stage.

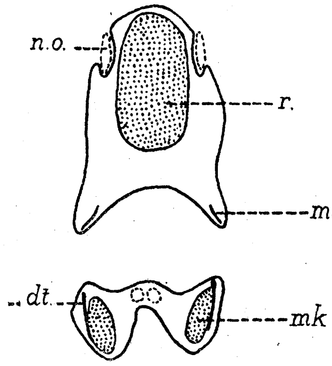

FIG. 3.—Transverse section through the anterior end of the ethmoid region of a 5-mm. larva, × 115.†

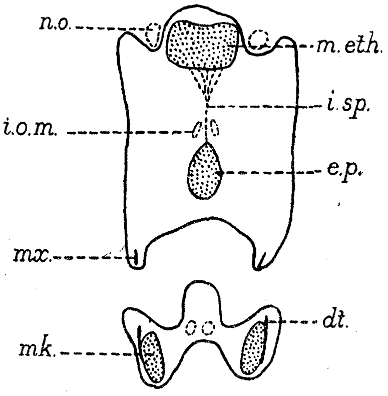

FIG. 4.—Transverse section through the posterior end of the ethmoid region of the same, × 115.

The supraorbital bars (figs. 1, 2, 5 and 6, *s.o.b.*) are strongly arched, rod-like bars of cartilage, roughly oval in transverse section, situated between the brain and the upper parts of the eyes. Anteriorly they are continuous with the mesethmoid cartilage, and posteriorly they are connected with the antero-dorsal edges of the auditory capsules. As a definite suture appears to be present at this stage between the cartilage of each bar and that of the corresponding auditory capsule (*cf.* fig. 6), it seems fairly certain that they do not arise as outgrowths from the anterior edges of the capsules. No cartilage is developed in the roof of the orbitotemporal region at this or any other stage. A transverse epiphysial bar, connecting the two supraorbital bars behind the epiphysis, is not present at any stage of development, nor is such a bar even indicated by thickenings or processes on the supraorbital bars.

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* WIJHE (1922, p. 284) has suggested that the terms "tropibasic" and "platybasic" are morphologically incorrect, and recommends their substitution by the terms "tropitrabic" and "platytrabic."

† All drawings of transverse sections made with camera lucida.

The membranous interorbital septum is well developed, but is very thin ; it is attached below to the dorsal edge of the trabecula communis, above to the thin membranous base of the brain cavity. In its posterior part the septum becomes much lower and also thicker as the brain cavity approaches the base of the chondrocranium in the region of the basicranial fenestra (fig. 5), and just behind this point it is entirely obliterated. The proximal ends of the rectus eye-muscles appear to be embedded in the connective tissue lying at the base of the brain cavity and surrounding the posterior end of the interorbital septum.

An independent ring of cartilage—the sclerotic—is developed round each eye (fig. 5, *scl.*).

As stated above, the trabeculæ merge insensibly into the parachordals, but for purposes of description it may be assumed that the posterior margin of the basicranial fenestra represents the line of division between these two cartilages. The anterior edge of the gasserion ganglion of the trigeminal nerve lies on either side between the parachordal and the posterior end of the supraorbital band where the latter joins the auditory capsule (fig. 6, *gs. g.*) ; the geniculate ganglion of the facial nerve (*gn. g.*) lies more ventro-medially, and is separated from the gasserion ganglion by the jugular vein (*j.v.*). The lateralis ganglion of the facial nerve is difficult to trace at this stage, but it appears to be more or less intimately connected with the gasserion. The greater part of the complex formed by the above-mentioned ganglia lies in a recess between the brain cavity and the ventro-lateral wall of the chondrocranium, *i.e.*, in a trigemino-facialis chamber (*cf.* fig. 6). The outer wall and floor of this chamber are formed by the anterior extension of the front of the auditory capsule, and by the prootic cartilage

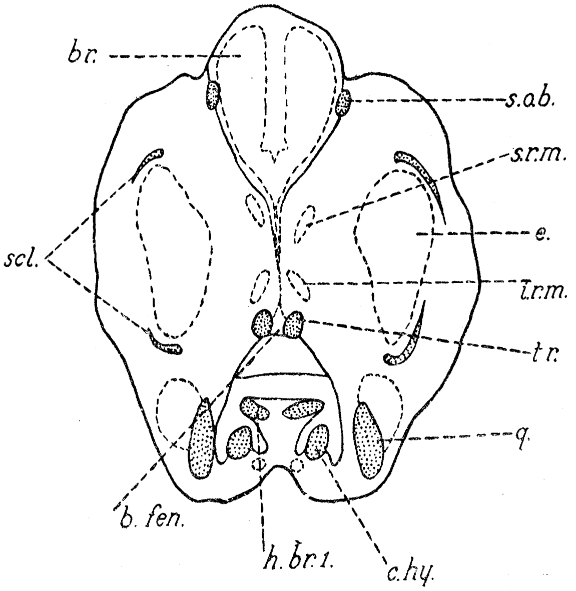

FIG. 5.—Transverse section through the interorbital region of a 5-mm. larva, × 115.

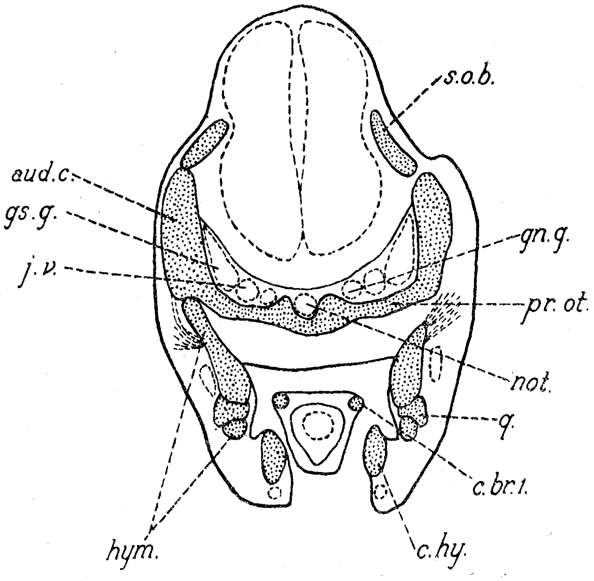

FIG. 6.—Transverse section through the postorbital region of the same, × 115.

respectively; the inner wall is provided by a thin membrane, which serves to separate the chamber from the brain cavity proper. All the branches of each trigeminal nerve appear to pass outwards in front of the prootic cartilage, between the anterior parachordal and the posterior end of the supraorbital bar.

The prootic cartilage is rather flat and plate-like, and separates the exits of the fifth and seventh nerves. It is impossible to state how this cartilage originates, since at this stage it is already joined medially to the anterior parachordal, and laterally to the base of the auditory capsule (figs. 2, 6, *pr. ot.*). Behind this cartilage is the narrow, slit-like facial foramen, which gives exit to the hyoideomandibular branch of the facial nerve, and to the jugular vein (fig. 2, *f.* VII).

The tip of the notochord is situated a little posterior to the basicranial fenestra. The parachordals have already united below its most anterior part, which rests on the surface of the basal plate thus formed. Opposite to the prootic cartilages the notochord is more deeply imbedded in the chondrocranial base, and a low ridge separates it on either side from the geniculate ganglion (figs. 2, 6, *not.*); a sheath of tissue, apparently of procartilaginous nature, protects its dorsal surface. Behind the foramina for the seventh nerve, the two parachordals become separated by a narrow fissure—interparachordal fissure—which widens somewhat posteriorly, and extends throughout the whole of the auditory and occipital regions of the chondrocranium. This fissure is entirely filled by the notochord, which is thus unprotected by cartilage dorsally and ventrally for the greater part of its length (fig. 7, *not.*). The parachordals (figs. 1, 2 and 7, *par.*) lie at about the same horizontal level as the bases of the auditory capsules anteriorly, and a little above them posteriorly; each is a rather thin, flat plate, which, even at this stage, cannot be divided into mesotic and occipital sections.

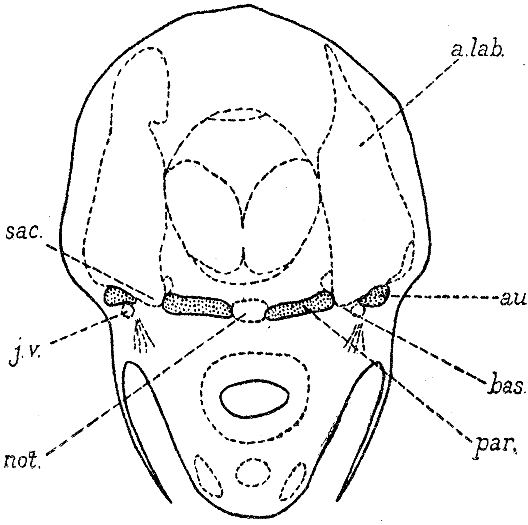

FIG. 7.—Transverse section through the auditory region of a 5-mm. larva, × 115.

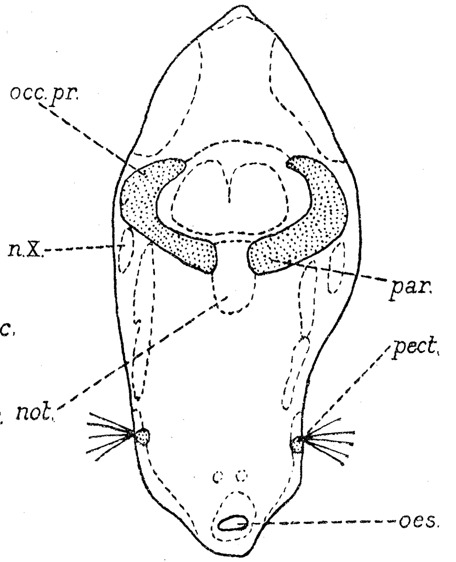

FIG. 8.—Transverse section through the occipital region of the same, × 115.

The front wall of the auditory capsule is already developed, and protects the anterior end of the membranous labyrinth, which lies opposite the foramen of the seventh nerve (fig. 6, *aud. c.*). The junction of the supraorbital bar with this capsular wall forms a rudimentary roof over this part of the labyrinth. The remainder of the auditory organ is protected by cartilage only at its base. This basal cartilage is connected with the parachordal anteriorly by a wide commissure behind the facial foramen (*cf.* fig. 2), but more posteriorly a broad basicapsular fissure separates the two cartilages (figs. 2, 7, *bas. fs.*). Just anterior to the front of this fissure a line of division between the cartilage of the capsule and that of the parachordal is still apparent in the structure of the tissue; further forward the two are indistinguishably fused. The sacculus of the auditory labyrinth (fig. 7, *sac.*) projects downwards into the basicapsular fissure, and is partly supported by the outer edge of the parachordal. The cartilage forming the base of the capsule gradually diminishes posteriorly, and ends abruptly opposite the exit of the glossopharyngeal nerve. Its hinder part bends inwards a little towards the parachordal, with which it is connected by a narrow strand of what appears to be procartilage, lying just behind the exit of the glossopharyngeal nerve. From the inner edge of the posterior part of the capsular base a small, pointed cartilaginous process projects upwards, and is continued dorsally as a vertical membranous pillar which lies between the lateral semi-circular canal and the remainder of the labyrinth. This little pillar is the rudiment of the lateral semi-circular septum, which becomes completed at a later stage (figs. 1, 2, *l.s. sp.*). The posterior semi-circular septum around which the corresponding canal runs is still in an entirely membranous condition.

In that part of the auditory region behind the exits of the glossopharyngeal nerves the parachordals are the only cartilages yet developed. The vagus does not yet emerge through a definitive foramen or fissure, but passes outwards over the outer edge of the parachordal. Although the cartilaginous base of the auditory capsule terminates opposite the ninth nerve exit, the labyrinth itself extends beyond the vagus exit into the occipital region.

Behind the cerebellum a layer of connective tissue in which a number of procartilage cells are apparent is present above the brain, but no true cartilaginous roof is present in the auditory region at this stage.

Posterior to the vagus exit the parachordals become somewhat expanded laterally, and the occipital processes arise from their outer edges and extend in an anteromedial direction above the brain, without, however, coming into contact to form a complete arch (figs. 1, 2 and 8, *occ. pr.*). The diameter of the notochord is considerably larger in this region, and the interparachordal fissure correspondingly wider (fig. 8, *not.*).

Visceral Arches.—The Meckel's and quadrate cartilages of the mandibular arch, and all the elements of the hyoid arch, are already well developed. Although definite articular fissures do not yet exist, the different cartilages are well differentiated, and the lines of division between them are clearly apparent.

Meckel's cartilage is massive, and tapers to a blunt point anteriorly, which lies a little in front of the anterior end of the rostrum (figs. 1, 3 and 4, *mk.*). It is roughly oval in transverse section, and, in common with most of the elements composing the first two arches, possesses a definite perichondrium. It is closely connected with the rather elongate quadrate (figs. 1, 5, *q.*), and, in the region of its articulation with that element, shows a marked retro-articular process. The quadrate is closely applied to the lower end of the hyomandibular, but here again the line of division between the two elements is clearly visible (*cf.* fig. 6, *q.*, *hym.*). The pterygoid and palatine parts of the upper jaw are as yet quite undeveloped, and no procartilaginous rudiments of these cartilages are apparent.

In the hyoid arch, hyomandibular (epihyal), interhyal, ceratohyal, and basihyal are already present. The hyomandibular is roughly triangular in shape; it is perforated in the middle by a small foramen which gives exit to the hyoideomandibular branch of the facial nerve (figs. 1, 6, *hym.*). The dorsal edge abuts against the lower surface of the auditory capsule from opposite the front end of the latter to the level of the commencement of the basicapsular fissure. The cartilage of the hyomandibular is separated from that of the cranium by richly cellular tissue. It is closely connected with the remainder of the hyoid arch by a small flattish interhyal (fig. 1, *i. hy.*), which is applied to its lower edge almost immediately below the foramen. The massive ceratohyal (figs. 1, 5 and 6, *c. hy.*) passes forwards inside the hyomandibular and quadrate, and is almost contiguous with its fellow anteriorly. No hypohyal elements are present, nor are they developed at any stage. A small rounded basihyal (fig. 1, *b. hy.*) lies above and between the tips of the ceratohyals, with which it is connected by thick deeply staining tissue.

Cartilaginous elements are developed only in connection with the first two branchial arches. The first arch consists on each side of an elongate, rod-like ceratobranchial (fig. 6, *c. br.* 1), to the anterior end of which is closely applied a shorter and broader hypobranchial (fig. 5, *p. br.* 1). A rather long basibranchial lies with its posterior end between the hypobranchials, and extends forward between the ceratohyals nearly to the basihyal, with which it is connected by a strand of richly cellular tissue. The second branchial arch consists of a pair of simple rod-like ceratobranchials.

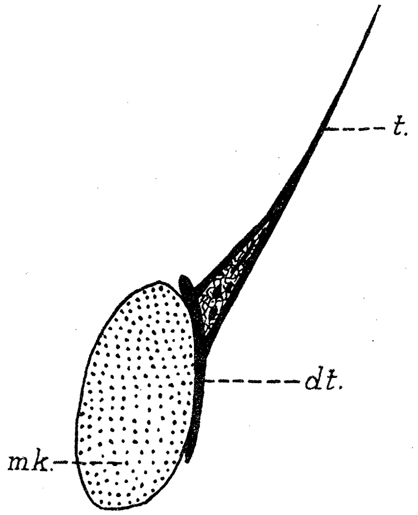

FIG. 9.—Transverse section through the anterior end of the lower jaw of a 5-mm. larva, × 383.

Even at this early stage two pairs of membrane bones are developed in connection with the jaws, namely, the maxillaries and dentaries. The exact extent of these bones is difficult to define owing to the poor state of preservation. Each maxillary (figs. 3, 4, *mx.*) bears three long, pointed teeth, which decrease in size from before backwards. There are two strong teeth anteriorly, which are placed close to one another; their expanded bases appear to be embedded in the connective tissue surrounding the tip of the rostrum. Each dentary (figs. 3, 4 and 9, *dt.*) is closely applied to the outer edge of Meckel's cartilage, and is armed with a strong tooth anteriorly, in addition to three lateral teeth similar to those of the maxillary.

Stage II.

The description of this stage is based on a reconstruction made from a larva of 11 mm.; serial sections of specimens of 13 mm. to 20 mm. were also studied.

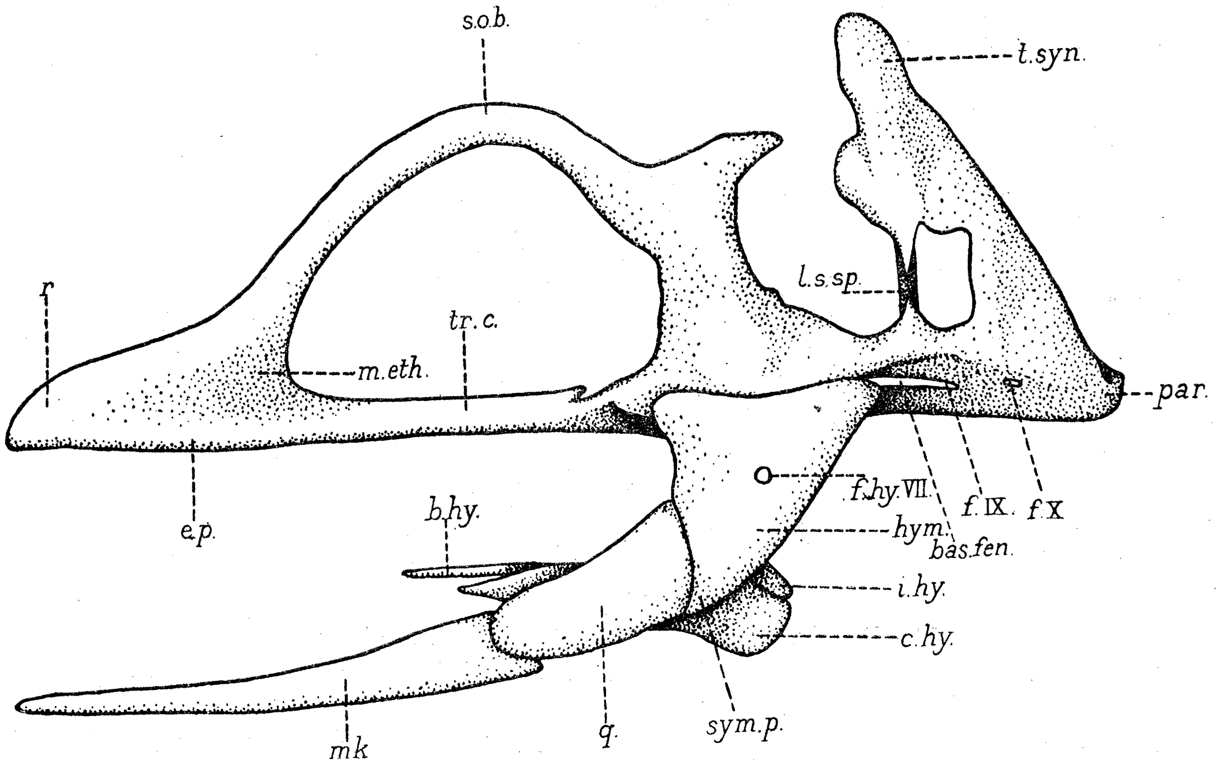

FIG. 10.—Lateral view of the chondrocranium of an 11-mm. larva of *Anguilla vulgaris*, × 97. The branchial cartilages are omitted.

Drawing made from a wax model 192 times the actual size of the chondrocranium.

Neurocranium.—The rostrum (figs. 10, 11, *r.*) is now longer and more acute, already foreshadowing the elongate character of that of the adult. The ethmoid plate appears somewhat broader, owing to the outgrowth of narrow horizontal ledges lying below the nasal organs. These organs (fig. 12, *n.o.*) still lie in simple pits, which are quite open to the exterior and are embedded in the embryonic connective tissue. The mesethmoid cartilage has become more hollowed out between these organs, and the thin, plate-like middle portion of its hinder end has extended posteriorly, and fills the position occupied by the anterior part of the interorbital septum in the previous stage. In the later larvæ of this stage (specimens H and I) this median partition has extended still farther back, and a small knob on the middle of its hinder edge gives attachment to the oblique eye-muscles (figs. 11, 12, *m. eth.*).

The trabecula communis is now a little broader, particularly at its posterior end (figs. 10, 11 and 13, *tr. c.*). Anterior to the basicranial fenestra there is a prominent ridge on its dorsal surface, which gradually diminishes anteriorly; this is continued posteriorly above the fenestra as a small, pointed process (*cf.* figs. 10, 11). The internal carotid arteries enter the cranium through the fenestra, and pass upwards on either side of this process. The position of the fenestra in relation to the hypophysis differs in the various specimens constituting this stage, being immediately below the hypophysis in an 11 mm. larva and posterior to it in larvæ of 13 and 17 mm. The hypophysis itself is much closer to the base of the cranium than in the previous stage.

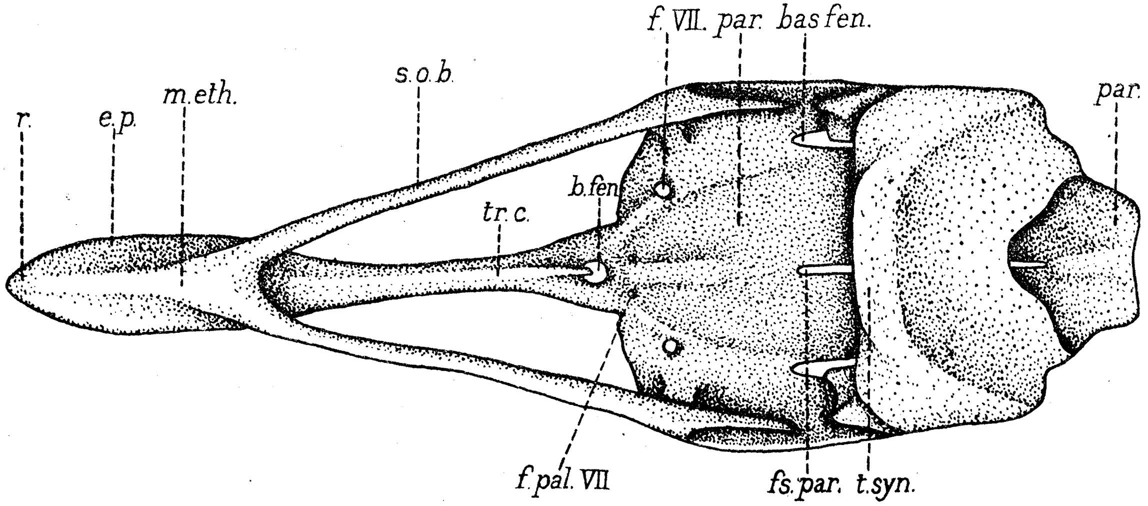

FIG. 11.—Dorsal view of the neurocranium of the same larva, × 97. Drawing made from a wax model 192 times the actual size of the chondrocranium.

The supraorbital bars (figs. 10, 11 and 13, *s.o.b.*) are a little deeper at this stage, especially in their posterior parts, where they have expanded towards the chondrocranial base. There is still no trace of a cartilaginous roof in the orbitotemporal region.

The optic nerves cross one another at the point where the interorbital septum joins the base of the brain cavity. This base is now formed by a thick pad of connective tissue, and the optic nerves pass through this pad without actually penetrating the interorbital septum. The rectus eye-muscles, as before, are attached to the connective tissue surrounding the posterior end of the septum, at a point just above the process over the basicranial fenestra. The optic, oculomotor, trochlear, and abducens nerves, as well as the greater part of the trigeminal, pass outwards between the trabecula communis and the supraorbital bar, *i.e.*, through a large optic fenestra.

The relations of the ganglia of the fifth and seventh nerves to the surrounding cartilages have undergone little change, but the development of a low ridge on the prootic cartilage (figs. 11, 14, *pr. ot.*) has separated the geniculate ganglion from the gasserion-lateralis complex and the jugular vein. Thus, the latter lie in a distinct trigemino-facialis chamber, but the geniculate ganglion is situated more medially between the base of the brain and the anterior parachordal plate. As in the previous stage, the branches of the trigeminal nerve do not exit through foramina in the chondrocranium ; the maxillo-mandibulary ramus passes downwards in front of the prootic cartilage at the point where it merges into the anterior parachordal, and the ophthalmic branch runs outwards below the posterior part of the supraorbital bar. The prootic cartilage is a little broader than in the previous stage, and the facial foramen circular instead of oval (fig. 11, *f.* VII). In addition to the hyoideomandibular ramus of the seventh nerve, and the jugular vein, the external mandibular branch of the lateralis part of this nerve also passes outwards through the facial foramen. The palatine ramus emerges through a minute foramen in the anterior parachordal, situated a little anterior to the facial foramen (fig. 11, *f. pal.* VII).

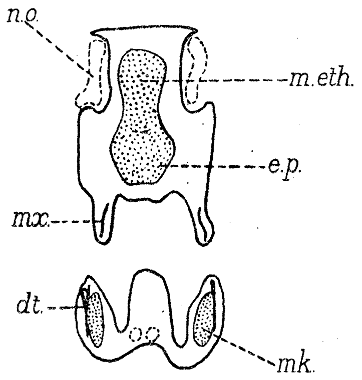

FIG. 12.—Transverse section through the middle of the ethmoid region of an 11-mm. larva, × 77.

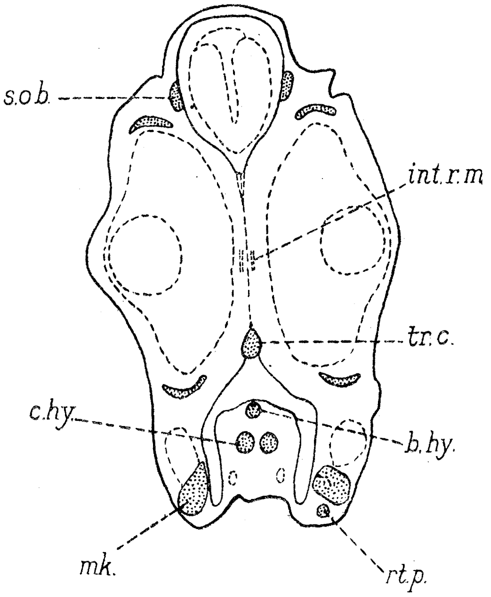

FIG. 13.—Transverse section through the interorbital region of the same, × 77.

The tip of the notochord now occupies a more posterior position, being behind the level of the facial foramen ; the region occupied by its anterior portion at the previous stage has been filled up by cartilage, so that a low median ridge is apparent on the dorsal surface of the anterior parachordal plate (*cf.* figs. 11, 14). This change in position of the tip of the notochord is not due to any actual shrinking of the latter, since careful measurement reveals an increase in length, but rather to a difference in the rate of growth of the notochord and of the surrounding cartilages. Just anterior to the tip of the notochord, a line of division between the two parachordals is still apparent. Cartilage has developed between the perichondria of the inner edges of the parachordals above the anterior part of the notochord, which thus lies in a groove in the ventral surface of the chondrocranial base (fig. 15, *not.*). More posteriorly, opposite the commencement of the basicapsular fenestra, this roofing cartilage disappears, and the notochord lies in an interparachordal fissure as in Stage I. This fissure is now considerably narrower, however, and does not reach to the hinder end of the cranium, the posterior part of the notochord being again roofed over by cartilage. In specimens H and I the notochord is covered dorsally by cartilage throughout its length.

A marked change has taken place in the relative position of the separate parachordals in this region; in the previous stage these cartilages occupied a horizontal position, and lay approximately on the same level as the bases of the auditory capsules, but their inner ends have been ventrally depressed so that the internal surface of the chondrocranial floor is now distinctly concave, and the bottom of this concavity lies at a level well below that of the bases of the capsules (compare figs. 7 and 15, *par.*). Behind the vagus exit, where the diameter of the notochord is considerably increased, the medial parts of these cartilages are correspondingly thicker. As mentioned above, a narrow band of cartilage connects the parachordals above the notochord in this region, and at the extreme posterior end of the cranium a similar ridge of cartilage is present below the notochord.

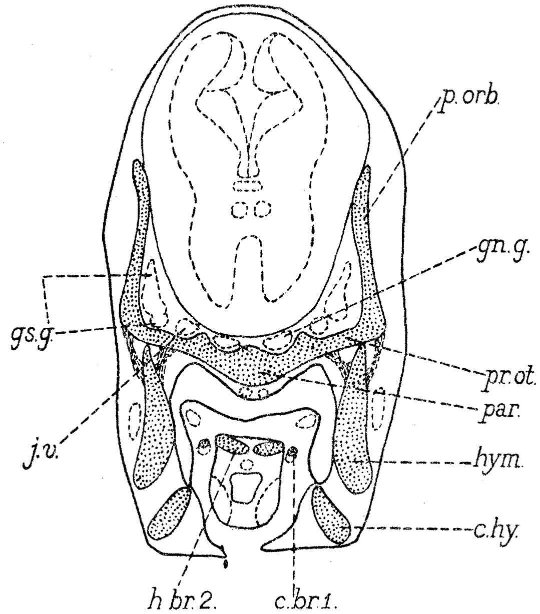

FIG. 14.—Transverse section through the post-orbital region of an 11-mm. larva, × 77.

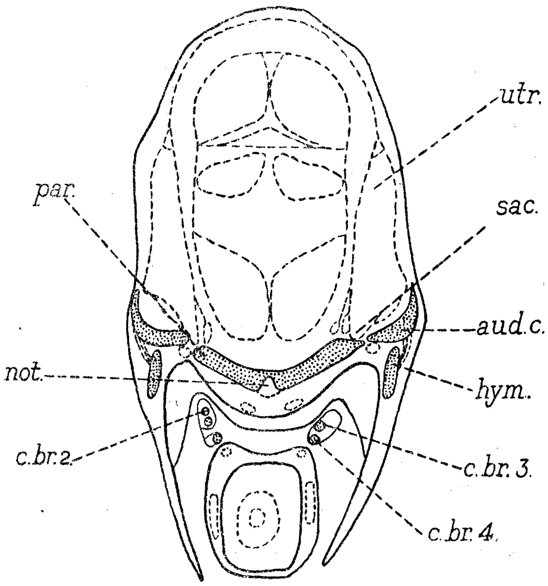

FIG. 15.—Transverse section through the middle of the auditory region of the same, × 77.

It is of interest to note that the growth of the different cartilaginous parts forming the more posterior regions of the neurocranium proceeds at a markedly disproportionate rate. For this reason the definition of orbitotemporal and auditory regions, although of convenience, is not accurate, since the boundary between these regions undergoes a certain amount of alteration during the ontogeny.* In a 5-mm. larva the notochord reaches well beyond the anterior end of the auditory labyrinth, and the exit of the palatine branch of the facial nerve lies just behind its tip, at a point near the anterior ends of the parachordals. In 13 and 17-mm. examples the tip of the notochord does not extend as far as the front of the labyrinth, and the palatine foramen is situated at some distance in front of its tip. Thus, the rate of growth of the lateral walls of the chondrocranium is proportionately greater than that of the basal parts, and a similar although less marked difference in rate of growth is apparent between the lateral and medial sections of the chondrocranial base. The slowing down of the growth of the middle parts of the cranium may be correlated with the posterior extension of the infundibulum, which occurs at this time, and which would restrict the growth of that portion of the cranial floor in its vicinity.

The auditory capsule has undergone considerable development since the previous stage, but, although its floor is almost complete, the outer wall and roof are still largely membranous. The outlines of the outer wall shown in the accompanying illustration (fig. 10) are somewhat irregular, but as true cartilage passes almost imperceptibly into procartilage and connective tissue, its limits are difficult to define.

The base of the capsule is firmly connected with the parachordal by two broad cartilaginous commissures; the more anterior of these, which was present in the earlier stage, has extended farther posteriorly, while the posterior commissure has replaced the strand of tissue behind the exit of the glossopharyngeal nerve. In this way, the wide basicapsular fissure of Stage I has become a narrow, elongate fenestra, which in a specimen of 11 mm. extends from a point just anterior to the lateral semi-circular septum to behind the ninth nerve (fig. 11, *bas. fen.*). This fenestra is closed for the whole of its length by procartilage, and the glossopharyngeal nerve passes outwards through its posterior end (fig. 10, *f.* IX). No trace of a suture is now to be seen between the cartilage of the anterior commissure and that of the parachordal, but such a line of division is apparent in connection with the posterior commissure.

The anterior part of the capsule is provided with a complete outer wall of cartilage, which surrounds the anterior semi-circular canal, while a narrow, posteriorly directed process forms a rudimentary roof (figs. 10, 11). There is no medial wall in this region, the cavity of the capsule communicating directly with the cranial cavity. No anterior semi-circular septum is present, nor is this ever developed. More posteriorly, in front of the lateral semi-circular canal, cartilage is largely wanting in the outer wall, and there is no roof to the capsule, but opposite the junction of the lateral semi-circular canal with the utriculus the upper part of the outer wall again becomes cartilaginous. From the inner face of this upper wall a horizontal ledge projects above the canal, and immediately below a sharp ridge is present on the capsular floor and separates the semi-circular canal from the remainder of the labyrinth (figs. 16, 17). A few sections farther back a narrow, vertical pillar of cartilage connects the ledge above with the ridge below.

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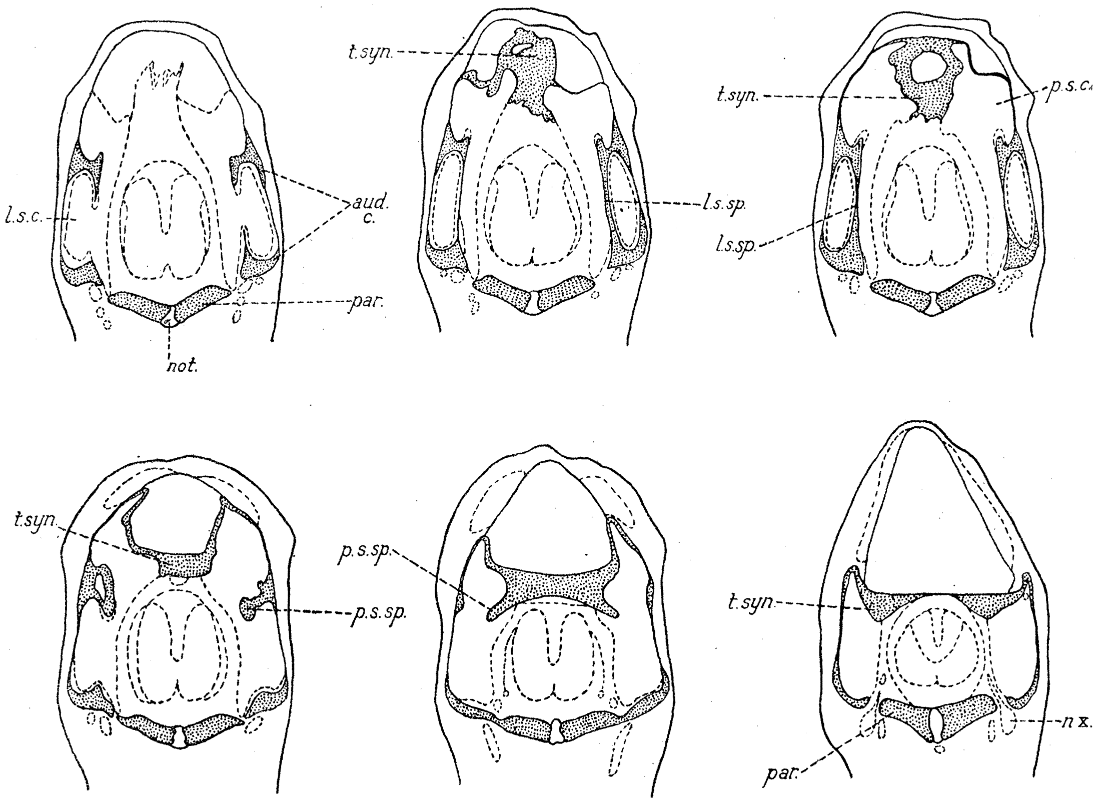
* A similar phenomenon has been observed in the chondrocranium of *Lepidosteus* (Veit, 1911).

This is the lateral semi-circular septum, which was indicated in the previous stage by a small projection on the floor of the capsule. The upper ledge merges farther back into the posterior semi-circular septum, around which runs the corresponding canal. This septum is now fully chondrified and runs obliquely upwards and inwards to join the synotic tectum (fig. 19, *p.s. sp.*).

Posterior to the lateral septum a large area in the side of the outer wall is not yet chondrified, but the upper parts of this wall appear to be composed of thin cartilage. Behind the glossopharyngeal exit, however, the outer wall is quite complete, and has fused with the occipital process described in Stage I. There is also a trace of an inner wall in the upper part of the capsule in this region, in the form of a narrow ridge of cartilage representing an extension backwards of the posterior semi-circular septum (fig. 20, *p.s. sp.*).



FIGS. 16 to 21.—A series of transverse sections (from before backwards) through the region of the synotic tectum of an 11-mm. larva, × 64.

In a 17-mm. larva the fenestræ in the outer wall have been largely filled up, and the cartilage forming the capsule has acquired a more or less definite perichondrium.

A roof of cartilage—the synotic tectum (figs. 10, 11, *t. syn.*)—is now present at the hinder end of the neurocranium. In specimen G (13 mm.) the anterior part of this tectum has the form of a thin plate of cartilage, situated vertically a little behind the posterior end of the cerebellum, and connected on either side with the cartilage of the auditory capsules (fig. 17). This plate seems to be composed of true cartilage, whereas the lateral connections are not yet fully chondrified. A few sections farther back the greater part of the plate disappears, and the roof is represented by a thick block of cartilage, above which is a large cavity representing an anterior continuation of the large space which lies above the nerve cord in the trunk region (figs. 18, 19). This portion of the roof is situated well below the level of the upper edges of the capsules, with which it is connected by bands of cartilage which surround the posterior semi-circular canals and form the lateral boundaries of the dorsal cavity mentioned above (figs. 19, 20). More posteriorly the tectum slopes steeply downwards towards the foramen magnum, and behind the vagus exit its central parts are again membranous.

In specimen H (17 mm.) the tectum extends forward to a point level with the exit of the auditory nerve. This anterior portion, which has arisen through the medial fusion of the auditory capsules above the hinder end of the cerebellum, merges posteriorly into that part of the roof which was developed in the younger example. The vertical plate of cartilage has disappeared, and a large space exists between the hind-brain and the chondrocranial roof; this space is partially occupied by portions of the auditory labyrinths. More posteriorly the tectum slopes rapidly downwards as in specimen G, and the space between it and the hind-brain is obliterated. The dorsal cavity above the synotic tectum remains the same as in the younger example.

On account of its form and position, it appears probable that the first part of the tectum, which is developed in specimen G, is formed largely by the anterior growth and medial fusion of the occipital processes described in the previous stage. The vertical plate of cartilage, which forms the anterior wall of the supracranial space, appears to arise independently.

Behind the synotic tectum a lateral wall of cartilage is present on either side of the occipital region, which partially surrounds the hind-brain brain (*cf.* figs. 10, 11). Farther back each of these walls becomes lower and finally disappears. A single pair of occipital nerves pass outwards above the hind ends of the parachordals, but do not pierce the lateral walls. The vagus nerve passes outwards through a large jugular foramen lying in the floor of the chondrocranium between the parachordal cartilage and that of the capsular base (figs. 10, 21, *n.* X).

No bones are yet developed in connection with the neurocranium.

Visceral Arches.—The different elements of these arches are still closely connected with each other, being separated merely by thin layers of richly cellular tissue which stains considerably darker than the cartilage.

The elongation of the anterior part of the neurocranium has been accompanied by a corresponding lengthening of the Meckelian cartilages. The anterior ends of these elements lie close together, and are connected by thick tissue. The retro-articular process (fig. 22, *rt. p.*) is now more marked, and a rudimentary coronoid process is also apparent. The position of the articulation between the Meckelian and quadrate cartilages appears to move anteriorly during this stage, being below the posterior part of the eye in a specimen of 11 mm. and a little in front of the middle of the eye in specimens of 13 and 17 mm. This apparent anterior movement of the point of articulation is due largely to an increase in length of the quadrate and hyomandibular cartilages, which are still closely connected with one another. The quadrate (figs. 10, 22, *q.*) is broadly rounded anteriorly, and no trace of the pterygoid and palatine parts of the upper jaw are visible.

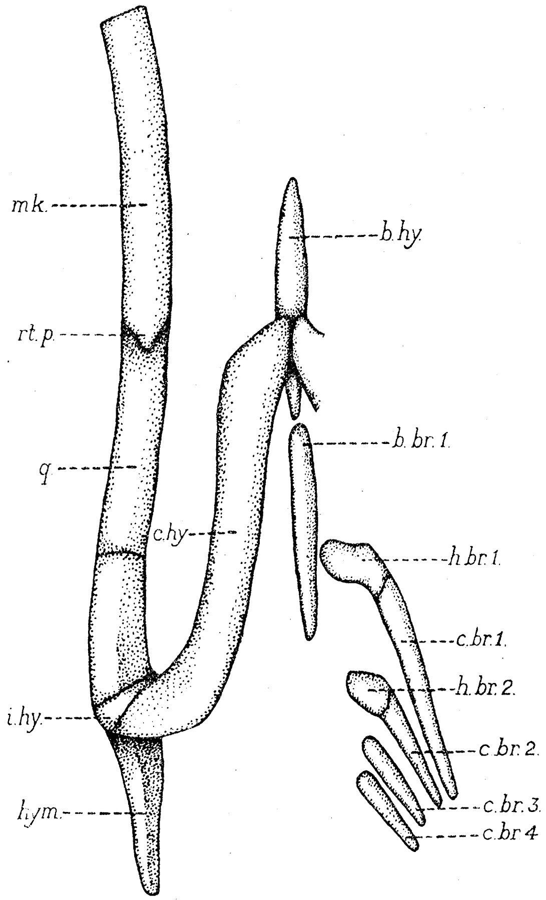


FIG. 22.—Ventral view of the visceral arches of an 11-mm. larva, × 210. The mandibular and hyoid arches are omitted on the right side, and the branchial arches on the left side. Drawing made from a wax model 250 times actual size.

A rudimentary inferior labial cartilage is represented by a densely cellular mass lying above the hinder end of Meckel's cartilage.

The upper articular edge of the hyomandibular is somewhat longer than in the previous stage, and it abuts against the neurocranium from the anterior end of the auditory capsule to a point opposite the commencement of the basicapsular fenestra (fig. 10, *hym.*). The anterior face of the hyomandibular is a little concave. The foramen which gives egress to the hyoideomandibular branch of the facial nerve now lies in the posterior half of the cartilage (fig. 10, *f. hy.* VII). In examples of 13 and 17 mm., a mass of cells situated near its posteroventral edge marks the commencement of an opercular cartilage corresponding to the opercular process of other Teleosts, and in a 20-mm. larva this element is completely chondrified. The lower end of the hyomandibular is continued ventral to the quadrate as a short, pointed symplectic process (fig. 10, *sym. p.*). The ceratohyal element is slightly longer than in the previous stage, and ends anteriorly in an acute point (figs. 10, 13, 14, and 22, *c. hy.*). The basihyal, which was represented in stage I by a mere nodule of cartilage, is now an elongate, narrow rod, which extends anteriorly well beyond the tips of the ceratohyals and ends at a point in front of the articulation of the Meckelian and quadrate cartilages (figs. 10, 13, and 22, *b. hy.*). Its posterior end lies just behind the tips of the ceratohyals, and is connected by thick tissue with the first basibranchial which is close behind (fig. 22, *b. br.* 1).

The first four branchial arches are now developed to a greater or lesser extent (fig. 22). The first two arches each consist of a hypo- and ceratobranchial on each side, the first hypobranchial being connected with the elongate basibranchial rod at a point just behind the middle of its length. The third and fourth arches are each composed of a pair of simple ceratobranchial rods. In the roof of the buccal cavity, where the epi- and pharyngobranchial elements later develop, there is as yet no sign of skeletal rudiments, but in a 20-mm. specimen these elements are indicated by masses of procartilage cells surrounding the posterior ends of the first and second ceratobranchials.

The maxillary and dentary bones are now well developed. The former (figs. 12, 23, *mx.*) extends posteriorly to a point behind the ethmoid region, and now bears four teeth. The strong anterior tooth is still independent of the maxillary. The dentary (figs. 12, 23, *dt.*) extends a little farther back than the maxillary, and bears five teeth, the anterior of which is canine-like.

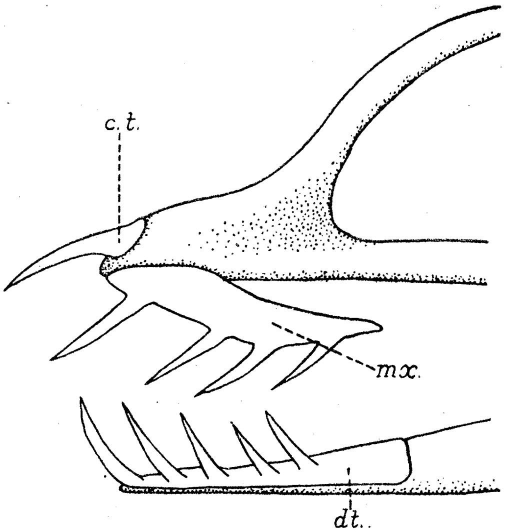


FIG. 23.—Reconstruction of the anterior region of the chondrocranium of an 11-mm. larva, with the maxillary and dentary bones in position, viewed from the left side, × 101.

Stage III.

The description of this stage is based on a reconstruction made from a larva of 31 mm.; serial sections and entire preparations of larvæ of 24 to 78 mm. were also studied.

Neurocranium.—The whole ethmoid region, and especially the rostrum, is much more elongate at this stage. The rostrum itself is considerably broader, and is roughly rectangular in transverse section (figs. 24, 25, *r.*). The ethmoid plate is wider in its posterior part, and the projecting ledges below the olfactory pits are more strongly developed (figs. 25, 26, *e. p.*). The hollowing out of the mesethmoid cartilage has proceeded farther and the thin median posterior portion has extended more posteriorly; the small projection which gives attachment to the oblique eye-muscles is more marked than in the previous stage (fig. 27, *m. eth. pr.*). From each postero-lateral edge of the ethmoid plate a narrow pillar of cartilage runs upwards and a little backwards to join the supraorbital bar at the point where the latter diverges from the thickened upper portion of the mesethmoid cartilage. These ectethmoid or antorbital cartilages arise as upgrowths from the dorsal surface of the ethmoid plate (figs. 24, 27, *ect. eth.*). In a 24-mm. example they are continuous with the ethmoid plate, but, although reaching the ventral edges of the supraorbital bars, they are not actually fused with them. In a 31-mm. example they pass imperceptibly into the bars.

The olfactory nerve (fig. 27, *n.* I), after leaving the bulbus olfactorius, which is closely applied to the cerebrum within the brain cavity, turns sharply downwards between the anterior parts of the eyes, and then proceeds horizontally forward; it passes between the ectethmoid cartilage and the posterior part of the mesethmoid, and finally bends outwards to ramify over the nasal organ. The nasal organ (fig. 26, *n. o.*) is now contained in a definite cavity which is shut off from the exterior for the greater part of its length. The ophthalmic branch of the trigeminal nerve runs external to and above the ectethmoid cartilage.

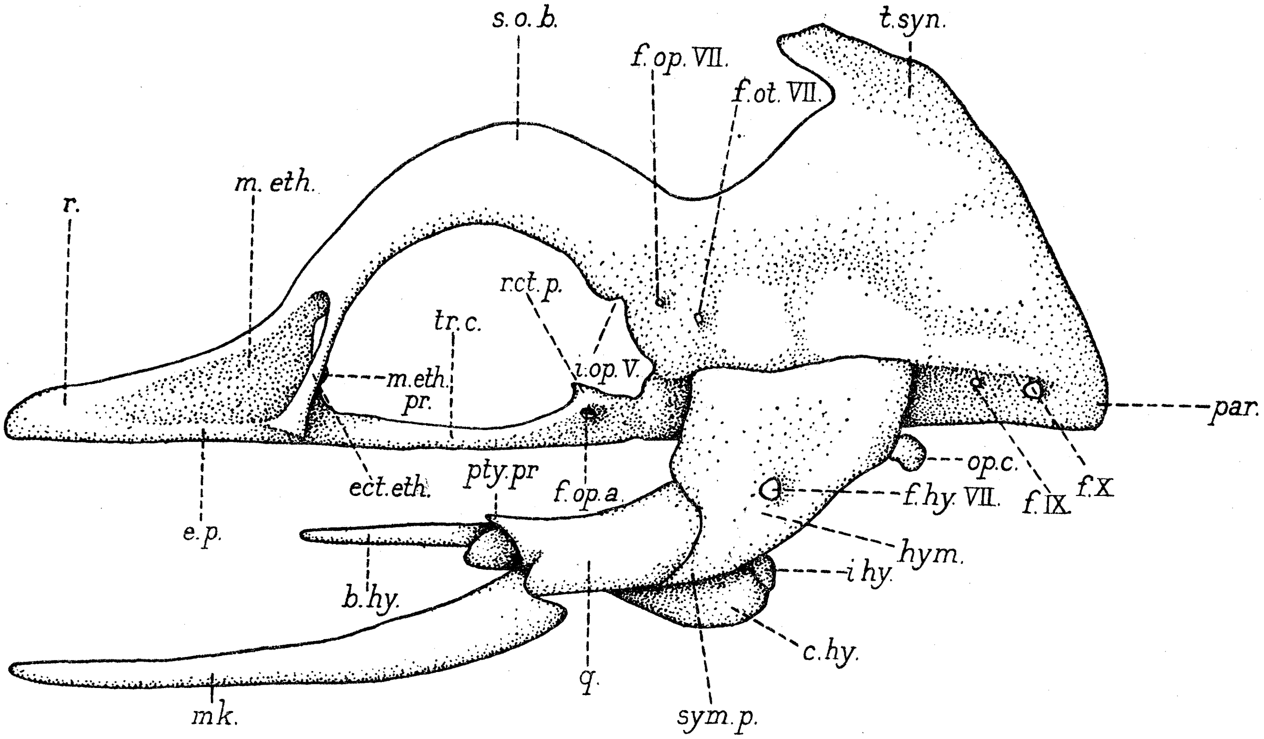


FIG. 24.—Lateral view of the chondrocranium of a 31-mm. larva of *Anguilla vulgaris*, × 49. The branchial cartilages are omitted.

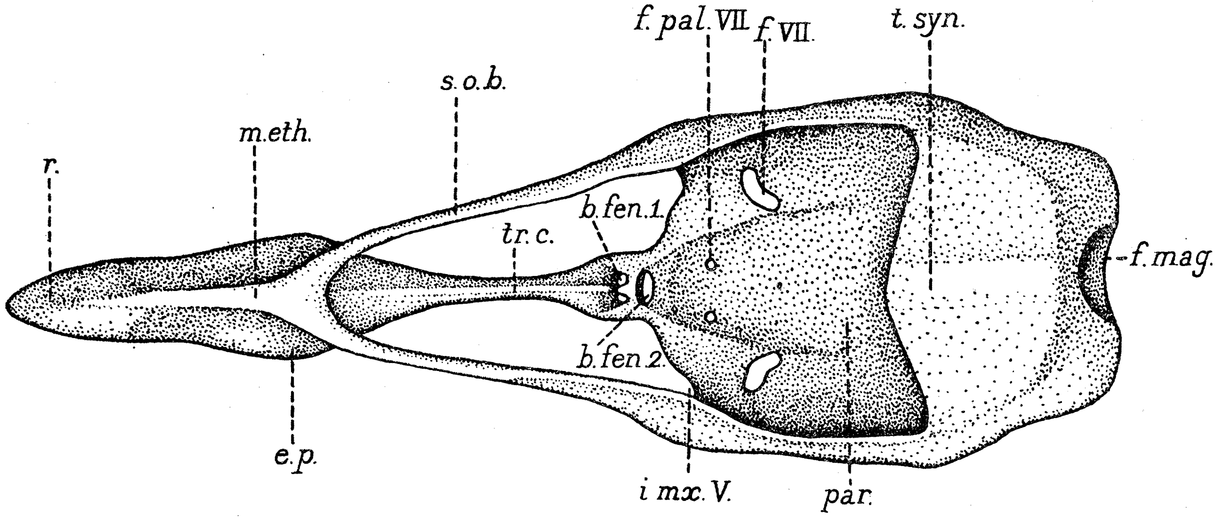


FIG. 25.—Dorsal view of the neurocranium of the same larva, × 49. Drawings made from a wax model 158 times the actual size of the chondrocranium.

The trabecula communis is now very narrow between the middle parts of the eyes, particularly in the older examples of this stage (figs. 24, 25 and 28, *tr. c.*). The basicranial fenestra* of the younger larvæ is now considerably larger, and the development of a transverse bridge of cartilage has divided it into two parts (fig. 29, A, *b. fen.* 1, *b. fen.* 2). The anterior of the two sections is the larger, and is more or less roofed over by cartilage, which has been formed from the small process which projected over the single fenestra in the previous stage. This process has grown out posteriorly, and has also expanded laterally and fused with the trabecular cartilages bordering the anterior fenestra. From the dorsal surface of this cartilaginous bridge over the fenestra, at a point level with the anterior edge of the latter, a small and short process projects forwards and upwards, and forms a basis for the attachment of the rectus eye-muscles (figs. 24, 29, A, *rct. p.*).

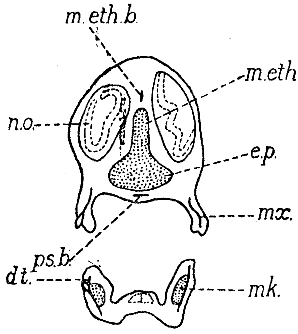


Fig. 26.—Transverse section through the anterior part of the ethmoid region of a 31-mm. larva, × 35.

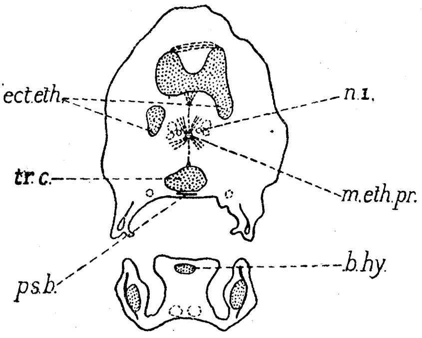


Fig. 27.—Transverse section through the posterior part of the ethmoid region of the same, × 35.

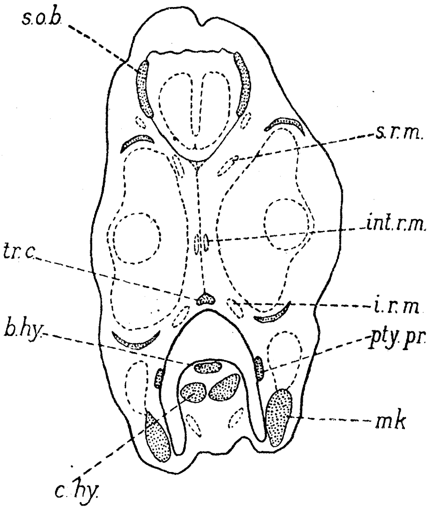


Fig. 28.—Transverse section through the interorbital region of the same, × 35.

The superior, inferior and internal pairs of muscles all converge between the posterior parts of the eyes, and run backwards for a short distance below the mass of connective tissue at the base of the brain cavity in this region; a little farther back they are joined by the external rectus pair, and the whole mass formed by their proximal ends is more or less intimately connected with the cartilaginous process mentioned above.

The relations of the internal carotids and other arteries to the cartilages in the region of the basicranial fenestræ are of some interest and may be briefly described. The internal carotid arteries (fig. 29, *int. c. a.*) pass forwards below the anterior parachordals and enter the cranium through the posterior basicranial fenestra, at which point they unite, to form

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* Torlitz (1922, p. 12, pl. IV, fig. 20) found no trace of any basicranial fenestra in a 66-mm. larva, and states that the inner edges of the trabeculæ are fused along their entire length.

a broad, median trunk (*int. c. a'.*). Just above the ventral bridge of cartilage separating the two fenestræ, this median trunk gives off a pair of small vessels—posterior cerebral arteries—which turn dorsally to enter the brain cavity (*p. cb. a.*). A little farther forward, below the roof over the anterior fenestra, the main internal carotid trunk receives the efferent pseudo-branchial arteries (*e. p. a.*), which run ventral to the trabeculæ and enter the cranium through the anterior basicranial fenestra. The median trunk

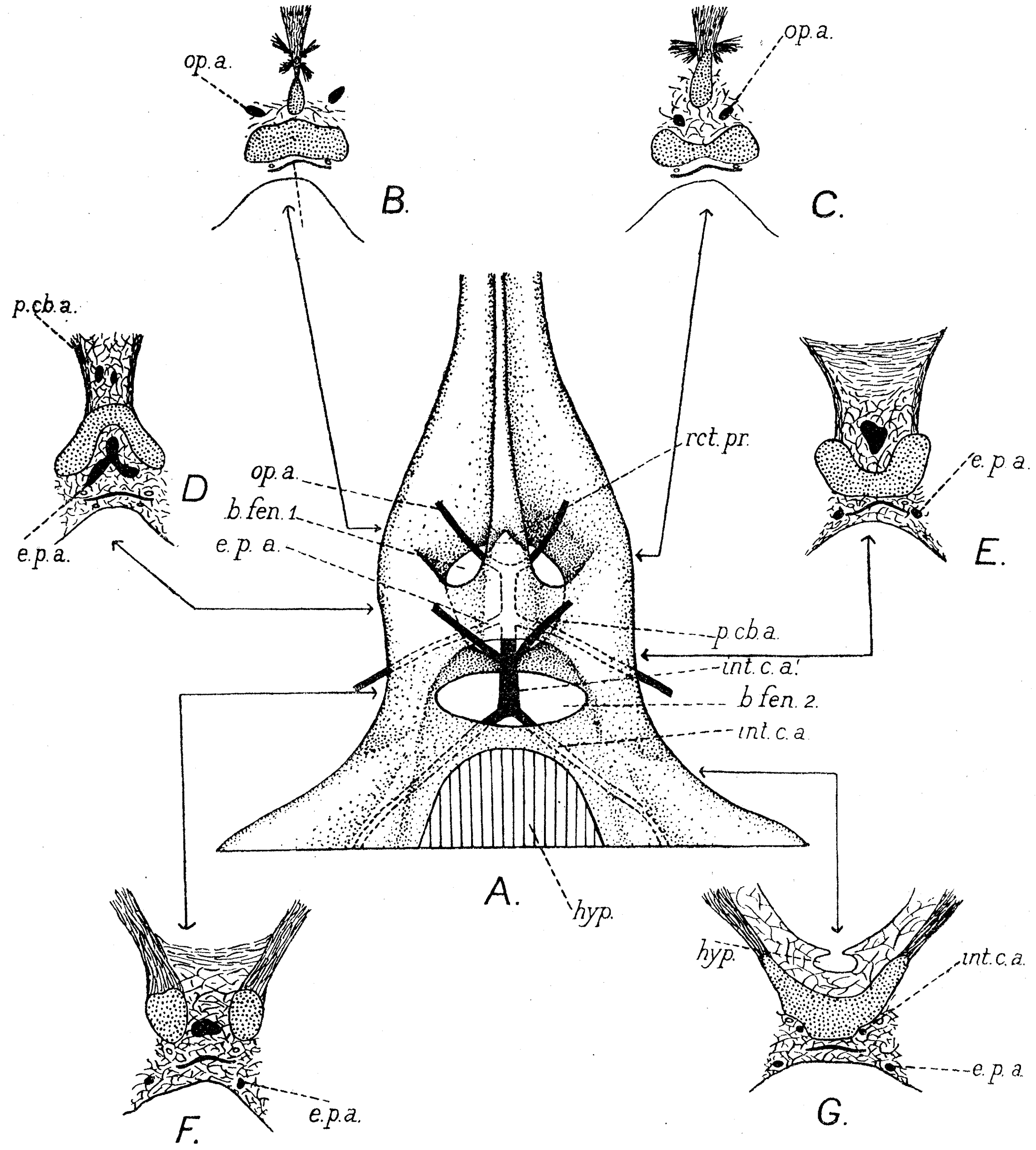

FIG. 29.—A, Reconstruction of the base of the chondrocranium in the region of the basicranial fenestræ of a 31-mm. larva, seen from above, showing the course of the internal carotid arteries and their branches, × about 200; B—G, transverse sections through the same region, × 82.

The continuous lines drawn from figures B to G to different parts of figure A show the region to which each particular transverse section corresponds. The course of the blood-vessels when running below the cartilage is denoted by dotted lines.

finally splits into two vessels, which pass forwards and upwards through the foramina on either side of the posterior part of the dorsal trabecular ridge, and run towards the eyes [ophthalmic arteries ? (fig. 29, *op. a.*)*].

The supraorbital bars (figs. 24, 25 and 28, *s. o. b.*) are thinner and distinctly deeper than in the earlier stages. Behind the orbits each band passes into the postorbital cartilage (figs. 24, 30, *p. orb.*) which forms the lateral wall of the cranium between the orbit and the auditory capsule. In the previous stages the extent of this postorbital wall was exceedingly small, and the anterior edge of the auditory capsule was situated close behind the orbit ; considerable growth of cartilage has taken place in this region, however, and the postorbital wall now extends from the exit of the trigeminal nerve to the facial foramen. Ventrally this wall is continuous with the prootic cartilage which has become somewhat broader. An inconspicuous parotic ridge on the outer edge of the base of the postorbital cartilage gives attachment to some of the muscles connected with the hyomandibular (*cf.* figs. **30**, **31**).

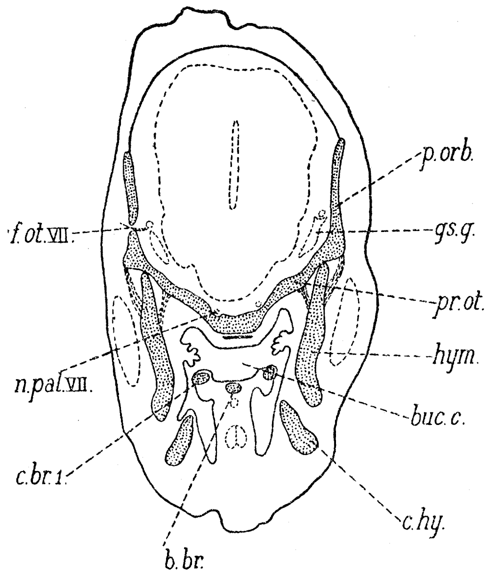

FIG. 30.—Transverse section through the anterior part of the postorbital region of a 31-mm. larva, × 35.

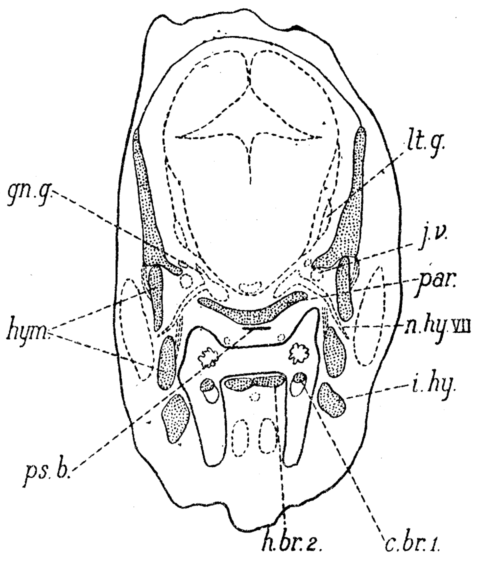

FIG. 31.—Transverse section through the region of the facial foramina of the same, × 35.

A well-marked indentation in the anterior edge of the prootic cartilage—the prootic incisure (fig. 25, *i. mx.* V)—marks the place of exit of the maxillo-mandibulary ramus of the trigeminal nerve, and another incisure in the ventral edge of the posterior part of the supraorbital band gives egress to the ophthalmic branch of the same nerve

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* In specimen N the posterior basicranial fenestra is divided into two equal parts by a longitudinal bridge of cartilage, so that each internal carotid enters the cranium through a separate foramen. This condition does not occur in any other specimens at any stage of development.

(fig. 24, *i. op.* V).* The anterior part of the postorbital wall is perforated by the ophthalmic branch of the facial nerve, which joins the corresponding branch of the trigeminal just inside the cranium (fig. 24, *f. op.* VII). A little more posteriorly another small foramen gives egress to the otic ramus of the facial nerve (figs. 24, 30, *f. ot.* VII). The closely related gasserion and lateralis ganglia lie within the postorbital wall just behind the second foramen. The complex is no longer contained in an extracerebral trigemino-facialis chamber as in the previous stage, nor is it separated from the geniculate ganglion; all the ganglia, together with the jugular vein, merely occupy the narrow space between the brain and the chondrocranial wall (*cf.* figs. 30, 31). The small foramen for the palatine ramus of the facial nerve (fig. 25, *f. pal.* VII) lies in advance of and medial to the large facial foramen. In the older examples of this stage (specimen O), a narrow bridge of cartilage has divided the facial foramen into two parts; the jugular vein and external mandibular ramus pass out through the anterior section, the hyoideomandibular ramus through the other.

The hypophysis (fig. 29, *hyp.*) is now situated behind both basicranial fenestræ, and close to the floor of the chondrocranium. The medial parts of the floor have been somewhat depressed in this region, so that the upper surface of the anterior parachordal plate is markedly concave (figs. 25, 30 and 31). Behind the facial foramina this concavity is still deeper, its lowest point being well below the level of the bases of the auditory capsules. In front of the notochord the two parachordals are completely fused, and form a solid plate of cartilage, which shows no trace of the median dorsal ridge described in the previous stage (fig. 32, *par.*). This plate is somewhat thinner than that of younger larvæ.

The anterior end of the notochord now lies very much farther back, and is situated just anterior to the lateral semi-circular septum in a 31-mm. specimen, and well behind it in one of 78 mm. As mentioned previously, accurate measurement shows that the notochord itself has undergone no actual decrease in length. The parachordals now meet above the entire length of the notochord, which thus lies in a groove in the ventral surface of the cranial floor. In a 31-mm. larva a line of division between the two parachordals is still apparent, but in all the older larvæ these cartilages form a solid plate. Posterior to the vagus exit another sheath of cartilage protects the notochord ventrally, but this never extends forward into the auditory region. In this enclosing of the notochord, cartilage extends from the inner edges of the parachordals, but no actual chondrification of the notochordal sheath takes place. In the younger examples of this stage the disproportionate rate of growth of the lateral and medial parts of the cranium is again marked in the auditory region, but this phenomenon becomes less apparent during the later stages of the ontogeny.

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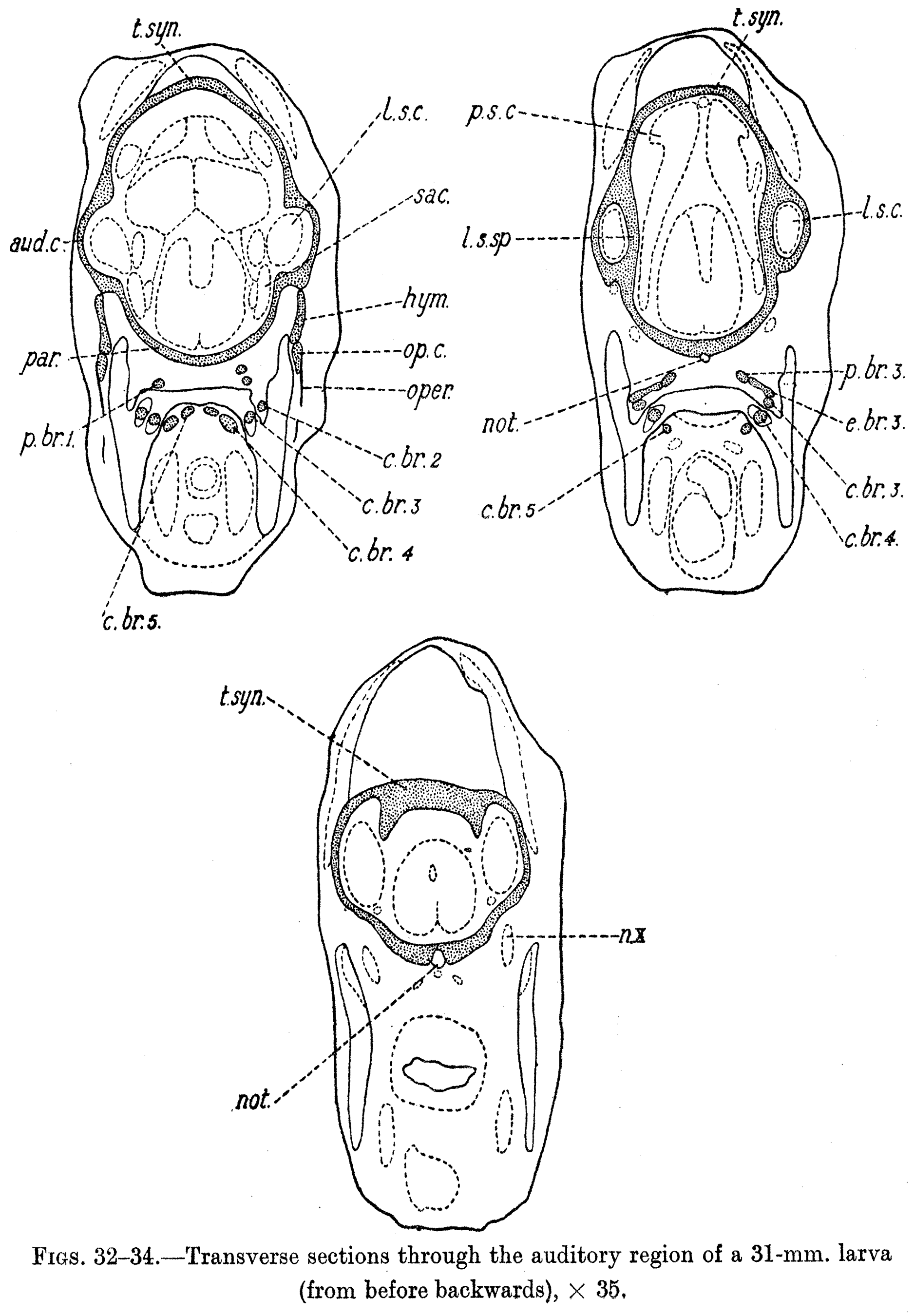
* TORLITZ (1922, pp. 12, 13, pl. IV, figs. 19, 20) describes and figures distinct foramina for the exit of these branches of the trigeminal nerve; the foramen for the ophthalmic branch is shown in the supraorbital band (*tænia marginalis*), and that for the maxillo-mandibulary branch is said to be situated "an der vorderen Grenze der Labyrinthregion." I do not find these foramina at any stage of development.

The auditory capsule has almost reached its maximum development, and forms a complete lateral wall to the cranium in this region, in addition to taking part in the formation of the cranial roof and floor. The cartilage of the capsule is closely moulded to the shape of the underlying labyrinth, and the course of the semicircular canals can be followed externally.



FIGS. 32–34.—Transverse sections through the auditory region of a 31-mm. larva (from before backwards), × 35.

The cartilage forming the base of the capsule is completely united with that of the parachordal plate throughout its length, and no trace of a suture is apparent. The small foramen, which gives exit to the glossopharyngeal nerve (fig. 24, *f.* IX), is situated a little anterior to and on the same horizontal level as the larger jugular foramen (*f.* X), and represents a remnant of the elongate basicapsular fenestra of the previous stage. The sacculus does not bulge out the cartilage of the capsular base to any extent, so that an external saccular bulla or internal fossa is scarcely indicated (fig. 32, *sac.*).

The anterior edge of the auditory capsule is about level with the facial foramen. As in the earlier stages, the roof is largely membranous in this region, and no medial cartilaginous wall or anterior semicircular septum is present. Behind the auditory nerve a strong prominence on the external face of the lateral wall, lying above the surface of articulation of the hyomandibular, marks the position of the lateral semicircular canal; this canal runs in a deep recess in the outer edge of the capsular cavity (figs. 32, 33, *l. s. c.*). The lateral semicircular septum is considerably stouter than before, and merges dorsally and ventrally into the cartilage of the capsular wall (fig. 33, *l. s. sp.*). The posterior septum is also stronger, and a moderate bulge in the roof above it marks the position of the corresponding canal externally. The hinder edge of the capsule is now level with the posterior border of the jugular foramen.

The synotic tectum is now completely fused on either side with the auditory capsules, and its postero-dorsal surface is convex rather than flat or concave as in the earlier stages (figs. 24, 25, 32, 33, 34, *t. syn.*). In a specimen of 31 mm. this roof extends anteriorly beyond the exit of the auditory nerves, in specimens of 40 and 45 mm. to a point just behind the facial foramina.

The lateral walls of the occipital region have undergone little change, and do not enclose any of the occipital nerves. A single pair of these nerves pass outwards above the hinder ends of the parachordals as before, the second pair lying immediately behind the posterior end of the cranium. Behind the tectum synoticum the upper boundary of the foramen magnum is formed by a slender bridge of fibrous connective tissue joining the lateral walls of the occipital region above the hind-brain.

The following membrane bones are present in connection with the neurocranium in a 31-mm. larva :—(1) A thin, vertical mesethmoid bone (fig. 26, *m. eth. b.*), situated medially above the mesethmoid cartilage and between the upper parts of the nasal organs ; (2) a well-developed parasphenoid (figs. 26, 27, 28, 30 and 31, *ps. b.*), extending from opposite the anterior ends of the nasal organs to a point level with the front of the auditory labyrinths. In a larva of 78 mm., a mass of cells below the anterior part of the ethmoid plate marks the commencement of the vomer. The nasals and frontals have also commenced to develop in this specimen, but no actual ossification of the cartilage has yet taken place.

Visceral Arches.—The lines of division between the different elements of the mandibular and hyoid arches are now clearly defined, particularly in the older examples of this stage. The cartilages are never widely separated by the intervention of tissue between them, and remain closely connected with one another by the richly cellular tissue mentioned in the descriptions of the earlier stages.

The perichondria of the two Meckelian cartilages are fused anteriorly for a very short distance, The coronoid process above the point of articulation with the quadrate is now more marked. A small pointed pterygoid process has grown forward from the antero-dorsal corner of the quadrate; this is very short, and passes anteriorly into a strand of connective tissue (figs. 24, 28, *pty. pr.*). No further development of cartilage in the pterygo-palatine portion of the upper jaw occurs at any stage of the ontogeny.*

The lower end of the hyomandibular is still closely applied to the quadrate, and the articulation remains quite immovable. The symplectic process (fig. 24, *sym. p.*) is a little longer than in Stage II. The dorsal edge of the hyomandibular is almost straight and shows little trace of two articular heads. It abuts against the neurocranium from a point in front of the facial foramen to the level of the lateral semi-circular septum. A well-developed opercular cartilage (figs. 24, 32, and 35, *op. c.*) is closely connected with its postero-ventral edge. This cartilage arises quite independently, instead of growing out from the hyomandibular as is the case in most bony fishes. The remainder of the hyoid arch is little changed, but the basihyal element (figs. 24, 28, and 35, *b. hy.*) has grown forward as far as the level of the ectethmoid cartilages in a specimen of 31 mm., and beyond them in older examples. The hinder end of this rod is somewhat broad and flat, and overlaps the anterior part of the basibranchial element immediately behind it (*cf.* fig. 35).

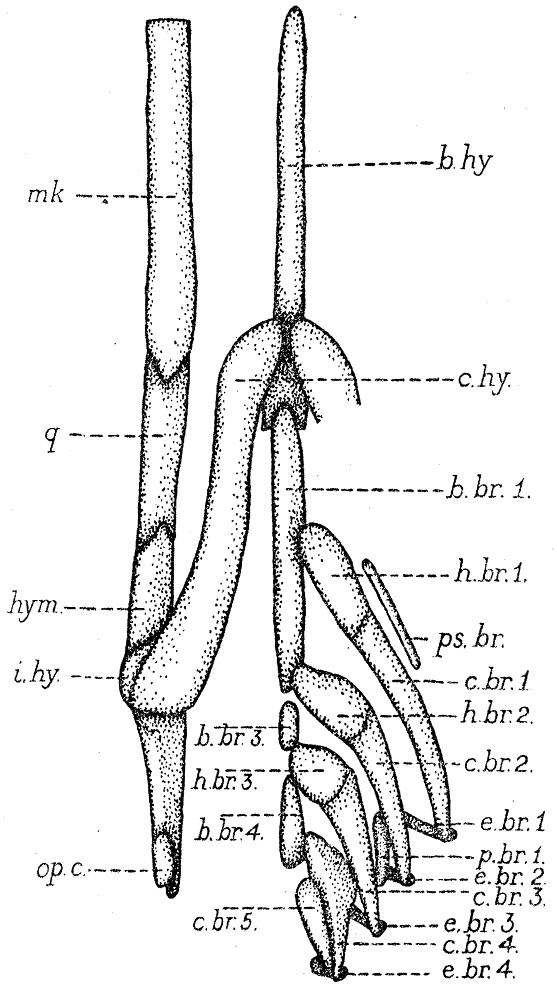


FIG. 35.—Ventral view of the visceral arches of a 31-mm. larva, × 71. The mandibular and hyoid arches are omitted on the right side of the figure, and the branchial arches on the left side. Drawing made from a wax model 316 times actual size.

One or more cartilaginous elements are now developed in connection with all the branchial arches, the first four arches consisting of basi-, hypo-, cerato-, epi- and pharyngobranchials; the fifth arch is formed by a pair of ceratobranchials (fig. 35). The first basibranchial cartilage has extended farther

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* TORLITZ (1922, p. 13, pl. IV, figs. 19, 21) describes and figures a complete palato-pterygo-quadrate cartilage in a 66-mm. larva. The palatine part is said to be connected with the ventral surface of the ethmoid plate.

posteriorly, and, in a 31-mm. larva, comes into contact with the hypal elements of the second arch. This elongate rod does not actually include the second basibranchial, however, since this arises in a 45-mm. specimen as a small, independent nodule of cartilage lying between the second pair of hypo-branchials and dorsal to the posterior end of the rod.

The first pharyngobranchial is represented by a rod-like cartilage lying below the parachordal (fig. 35, *p. br.* 1), which is connected with the upturned hinder end of the corresponding ceratobranchial by a small, curved epal element (*e. br.* 1) situated obliquely in the lateral wall of the buccal cavity. This pharyngobranchial is continued for a short distance posteriorly beyond its articulation with the epal cartilage, and is closely connected with the epibranchial and very small pharyngobranchial of the second arch. The third pharyngobranchial is quite free anteriorly, but is in close contact posteriorly with the corresponding element of the fourth arch, the two forming a practically continuous bar of cartilage. The basibranchial element of the third arch is very short (*b. br.* 3), while that of the fourth is longer and comes into contact with the ceratobranchials of the last arch (*b. br.* 4, *c. br.* 5).

In a specimen of 31 mm., a narrow, rod-like pseudobranchial cartilage is present above the anterior part of the first arch (fig. 35, *ps. br.*); in older examples two or three of these cartilages are developed.

The maxillary bone now extends almost to the tip of the cartilaginous pterygoid process, and bears about seven lateral teeth, in addition to the larger anterior tooth which has now become attached to the bone. Another small tooth has developed in front of this, and is quite independent of the maxillary, its base being embedded in the tissue above the tip of the rostrum. No præmaxillary bones are present in a specimen of 31 mm., but in larvæ of 40 to 78 mm. the rudiments of these bones are apparent. They lie above the rostrum, and have the form of incomplete bony tubes, each of which surrounds a sensory canal; these tubes unite posteriorly just in front of the mesethmoid bones (fig. 36, *pmx.*).* In the lower jaw the articular bone has now appeared, and is overlapped anteriorly by the hinder end of the dentary, which now bears seven teeth. Several of the bones forming the opercular series arise during this stage. The opercular bone itself is closely applied dorsally to the opercular cartilage (fig. 32, *oper.*).

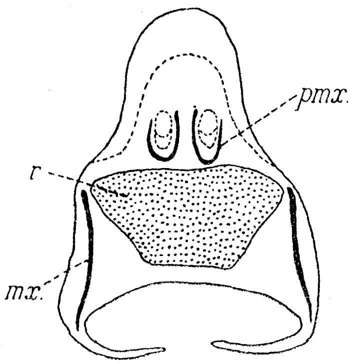

FIG. 36.—Transverse section through the anterior end of the ethmoid region of a 78-mm. larva, × about 85.

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* During the metamorphosis of the *Leptocephalus* and the early growth of the Elver the præmaxillaries, the mesethmoid, and the vomer become fused to form a single bone (*cf.* REGAN, 'Ann. Mag. Nat. Hist.,' Ser. 8, X, 1912, p. 378).

Metamorphosis Stages.

In connection with these stages, only the further changes undergone by the cartilaginous parts of the chondrocranium prior to their ossification are here described, and the development of the cranial bones is left largely out of consideration. It was found convenient to make a reconstruction of a 70 mm. larva, representing a comparatively early stage in the metamorphosis, and a brief description of the chondrocranium of this specimen is given below. In addition, serial sections of larvæ of 71 mm. and 64 mm., representing respectively earlier and later metamorphosis stages, were studied.

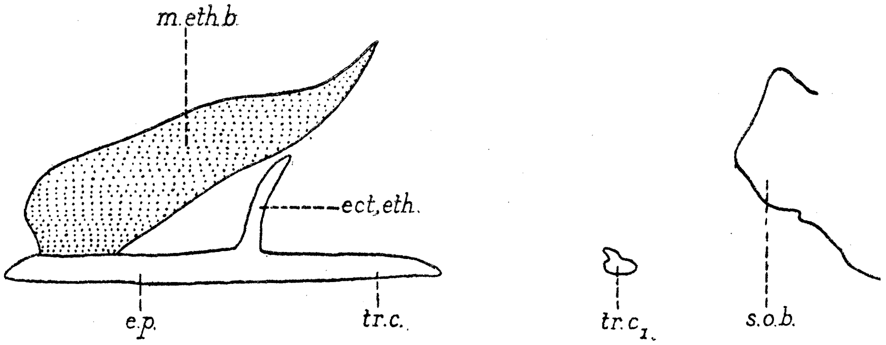

FIG. 37.—Outline reconstruction of the cartilaginous parts of the ethmoid and orbitotemporal regions of a 70-mm. larva, together with the mesethmoid bone; seen from the left side; × about 42.

Neurocranium.—In the ethmoid region a large part of the cartilage present in the early stages has been suppressed, the entire mesethmoid, the greater part of the rostrum, and the lateral portions of the ethmoid plate having entirely disappeared. The anterior part of the ethmoid plate is cleft by a narrow, median fissure, in which are situated the posterior ends of the præmaxillaries and the front part of the base of the mesethmoid bone (*cf.* fig. 38). This bone (figs. 37, 39, *m. eth. b.*) has extended ventrally towards the ethmoid plate, and has to a large extent functionally replaced the mesethmoid cartilage in providing a vertical septum between the nasal organs (fig. 39).

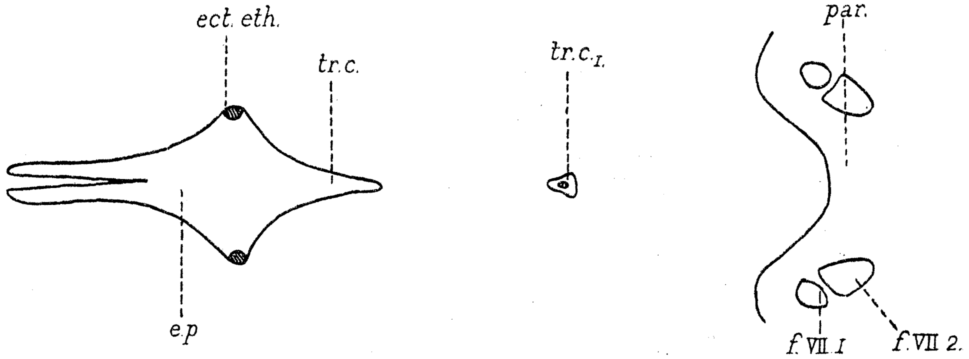

FIG. 38.—The same, seen from above. Cartilage is shown white; the mesethmoid bone dotted.

The upper parts of the ectethmoid cartilages have entirely disappeared, as well as the supraorbital bars, so that the remains of each ectethmoid appears as a short pillar projecting from the posterolateral edge of the ethmoid plate (figs. 37, 38, *ect. eth.*). They exhibit signs of breaking down still further, and, indeed, in the older larva they have entirely disappeared, together with the adjacent parts of the ethmoid plate.

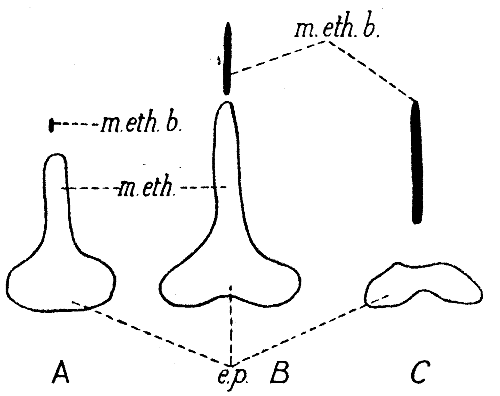

FIG. 39.—Transverse sections through the mesethmoid cartilage and bone between the nasal organs in A a 31-mm. larva, B a 78-mm. larva, and C a 64-mm. larva (late stage in the metamorphosis); × 61. Diagrammatic.

The oblique eye-muscles have their proximal ends inserted in the thick connective tissue lying between the lower edge of the hinder end of the mesethmoid bone and the cartilage of the trabecula communis, at a point just behind the ectethmoids.

The paired nasals and the vomer have been added to the series of membrane bones now present in the ethmoid region.

In the orbitotemporal region, the greater part of the supraorbital bars and trabecula communis, as well as a portion of the anterior parachordal plate, have been entirely suppressed, so that the anterior and posterior regions of the neurocranium are separated by a wide gap (*cf.* figs. 37, 38). The anterior part of the trabecula communis may be recognised as a pointed, posteriorly directed projection from the ethmoid plate (figs. 37, 38, *tr. c.*), which extends nearly to the optic chiasma. Behind this point the lower end of the interorbital septum is attached to the connective tissue surrounding the parasphenoid. The septum, which is still entirely membranous, is considerably stouter than in the earlier stages. In the region previously occupied by the anterior basicranial fenestra, a small, isolated piece of cartilage still remains at the base of the cranium; this represents a portion of the cartilaginous roof which was developed above the anterior basicranial fenestra in Stage III (figs. 37, 38, *tr.* c_1.). The small, anteriorly directed process with which the proximal ends of the rectus eye-muscles are associated still remains, and has not disappeared in the oldest larva of this stage.

The supraorbital bars are almost entirely absent, only their extreme posterior ends where they join the postorbital walls being still intact (fig. 37, *s. o. b.*). Portions of the cartilage at the posterior end of the postorbital wall have been replaced by the developing sphenotic and prootic bones.

Of those portions of the orbito-temporal region of the chondrocranium which have been suppressed no trace remains. They have been replaced functionally by the developing membrane bones: the supraorbital bars by the frontals, the trabecula communis and anterior parachordals by the parasphenoid.

In the auditory and occipital regions the cranium has undergone little change. The bones of the otic and occipital series have begun to develop, and the otic bones have replaced certain portions of the cartilaginous capsular walls. The parachordals are considerably thinner at this stage.

Visceral Arches.—Comparatively little change has taken place in the mandibular and hyoid arches, but the different elements are now more or less definitely separated by clear articular fissures. MECKEL'S cartilage is considerably longer, and the point of articulation with the quadrate now lies behind the eye. No further development of cartilage has taken place in the upper part of the mandibular arch; indeed, the pterygoid process is actually shorter, and in the older example is represented merely by a knob on the anterodorsal edge of the quadrate. The hyomandibular is no longer closely connected with the quadrate, the two cartilages being separated by a well-defined suture. The upper part of the hyomandibular has grown out posteriorly, and its dorsal surface shows distinct anterior and posterior articular heads.

The upper ends of the branchial arches have undergone a marked change in position with regard to the neurocranium; in Stage III the epibranchial of the first arch lay below the exit of the auditory nerve, but this cartilage is now situated ventral to the jugular foramen. This change in position has been brought about by the growth and consequent elongation of the cartilages forming the lower end of the arch, and especially of the ceratobranchial. The fifth arch still consists only of a pair of ceratobranchials.

A number of bones have now appeared in connection with the mandibular and hyoid arches. The slender larval teeth, with which the maxillary and dentary were armed at the last stage, have completely disappeared; the adult teeth are not yet apparent.

PART II.

OBSERVATIONS ON THE COMPARATIVE MORPHOLOGY AND DEVELOPMENT OF THE CHONDROCRANIUM IN BONY FISHES.

I. *The Ethmoid Region.*

A. *Ethmoid plate; mesethmoid cartilage and bone; rostrum, etc.*—The *ethmoid plate,** which forms the basis of the ethmoid region of the chondrocranium, arises in all Teleosts through the direct fusion of the anterior ends of the trabeculæ. In *Amia* and *Lepidosteus* the trabeculæ are at first connected anteriorly by a narrow, transverse bar—*trabecular commissure,* which later expands to form the ethmoid plate; this stage appears to be either very transitory or entirely omitted from the teleostean ontogeny.

The shape of the plate varies greatly in Teleosts, two extremes being the broad, trough-like plate of the Clupeidæ, and the narrow, elongate rod which represents the same element in the Syngnathidæ. The anterior border may be evenly truncated, rounded, or obtusely pointed, or it may be provided with a pair of anterolateral projections—præ-ethmoid cornua (SWINNERTON, 1902, p. 514). In *Gasterosteus* these projections give

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* "Subnasal lamina," PARKER, 1873; "rostral plate," MCMURRICH, 1883; "planum orbitonasale," VEIT, 1911; "Trabekelhörn," UHLMANN, 1921.

attachment to the anterior ends of the palatine cartilages, but in other forms (*e.g.*, *Amiurus*, *Ictalurus*) the cornua, although prominent, have no connection with the upper jaws.

A curious modification of the ethmoid plate occurs in early embryos of *Syngnathus* (KINDRED, 1921, p. 427). In an 8-mm. specimen the anterior half of the plate is bent upwards at right angles to the hinder part; in a 12-mm. specimen the front part has become straightened out, carrying with it the palatine cartilages which are connected with the well-developed præ-ethmoid cornua.* In embryos, ranging from 9 to 15 mm. in length, of the related genus *Siphonostoma* I find no trace of this phenomenon, nor has anything analogous to it been described in any other fish.

At the hinder end of the plate another pair of lateral projections are usually developed,† which later give rise to the ectethmoid cartilages. These processes are at first closely approximated to the anterior cornua, but the subsequent elongation of the ethmoid plate carries them far apart.

The remainder of the cartilages forming the ethmoid region nearly always appear comparatively late in the ontogeny. The fore-brain is usually situated at first either above or on the ethmoid plate, but as soon as this is withdrawn posteriorly a median wall of cartilage develops, which separates the nasal fossæ—*mesethmoid cartilage.*‡ This cartilaginous partition is sometimes broad and massive (*Galaxias*, *Amiurus*, *Callionymus*, *Cyclopterus*, etc.), extending to the lateral edges of the plate; in most bony fishes, however, it is hollowed out on either side to provide a pair of pits which lodge the nasal organs—*nasal fossæ* (GAUPP, 1906). The floor of each fossa is generally formed by a lateral outgrowth from the ethmoid plate ("cornua trabeculæ," PARKER, 1873; "solum nasi," GAUPP, 1906). These lateral extensions of the plate are particularly marked in *Cyclopterus* (UHLMANN, 1921—"processi antorbitales"). In many fishes the centre of the mesethmoid cartilage is hollowed out by a canal which lodges the proximal ends of the oblique eye-muscles (*q.v.*).

The development of the mesethmoid cartilage in *Amia* is of interest (PEHRSON, 1922). In a 12-mm. larva a short median process projects upwards from the ethmoid plate between the olfactory nerves. This process is broader posteriorly, and divides into a pair of low ridges which diverge in a postero-lateral direction and merge into the ectethmoid cartilages. In a 19½-mm. specimen this process is higher anteriorly, but in one of 21½ mm. it has entirely disappeared together with a large part of the hinder portion of the septum. Shortly afterwards a low and elongate mesethmoid cartilage is developed, which is similar to that of most teleostean fishes. Such an appearance of a temporary mesethmoid cartilage is quite unusual and is difficult to explain; possibly the anterior, dorsally projecting portion is connected with the laying down of the rudiments of the præmaxillary bones, which arise at a time when it has reached its maximum development.

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* "Rostral processes," KINDRED, 1921.

† "Parethmoid cornua," SWINNERTON, 1902.

‡ "Internasal septum," PARKER, 1873; "septum nasi," GAUPP, 1906; "septum rostri," VEIT, 1911.

The complete suppression of the mesethmoid cartilage, and its subsequent replacement functionally by the corresponding bone, which takes place during the metamorphosis of *Anguilla*, has not been described in any other fish. The disappearance of the cartilage may be due to the inward growth of the nasal organs, which become enlarged as the time of metamorphosis approaches. It will be of interest to describe briefly the development of the mesethmoid bone in a few other fishes.

In *Amia* and *Lepidosteus* it develops as a membrane bone which is quite independent of the cartilage, from which it is generally separated by a space filled with connective tissue (KINDRED, 1919, p. 31). In certain Teleosts this bone acquires a connection with the mesethmoid cartilage, either by the extension of the ossification into the underlying cartilage as in *Gasterosteus* (SWINNERTON, 1902, p. 521), or by the appearance of an independent perichondrial ossification which later fuses with the dermal portion. This double origin of the mesethmoid bone is found in *Amiurus* (KINDRED, 1919), and also in the Characinidæ and Cyprinidæ (SAGEMEHL, 1885, 1891), where the degree of ossification of the cartilage varies to a considerable extent. In the remainder of the Teleosts which have been studied, the bone is entirely dermal in *Salmo* (GAUPP, 1906) as in *Anguilla;* in *Trigla* (ALLIS*) and *Cyclopterus* (UHLMANN, 1921) a portion of the cartilage is invaded by bone ; in *Scomber* (SWINNERTON, 1902) the bone has lost all trace of its membranous origin and consists entirely of ossified mesethmoid cartilage.†

In the Syngnathidæ the relations of the mesethmoid cartilage to the ethmoid plate present a somewhat specialized condition. In *Siphonostoma* the mesethmoid cartilage appears comparatively late and arises quite independently of the plate (fig. 40, A, *m. eth.*). In the oldest stage in my possession this cartilage has commenced to ossify anteriorly, but its hinder portion is still largely procartilaginous, and, although it comes into contact with the ethmoid plate, shows no sign of fusing with it. In *Syngnathus* (KINDRED, 1921) no trace of a mesethmoid cartilage is apparent in specimens of 8 and 12 mm., the nasal organs being separated by a wall of fibrous connective tissue which lies above the ethmoid plate and forms an anterior continuation of the interorbital septum. This wall of tissue is later replaced by an "osseous ridge" (*t.c.*, p. 444), which is without doubt the mesethmoid bone. The condition in *Syngnathus* would seem to be even more specialized than that found in the related *Siphonostoma*, the cartilaginous mesethmoid being altogether omitted from the ontogeny.

In certain Teleosts an independent piece of cartilage is developed on either side above

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* ALLIS, E. P., "The Cranial Anatomy of the Mail-Cheeked Fishes," 'Zoologica,' XXII, Heft 57, 1910, 219 pp., 8 pls.

† This bone has received a number of different names, generally applied with little regard to the terminology employed and frequently without knowledge of the manner of its development :—"mesethmoid," McMURRICH ("The Osteology of *Amiurus catus* (L.) Gill," 'Proc. Canad. Inst.,' II, 1884, pp. 270–310, pl. II); "super- or supraethmoidal," PARKER, 1873, GAUPP, 1906—*Salmo*; "ethmoidale medium," GEGENBAUR ("Ueber das Kopfskelet von *Alepocephalus rostratus*," 'Morph. Jahrb.,' IV, 1878, Supp., pp. 1–40, pls. I–II); and "ethmoid," SAGEMEHL, 1884—*Amia.*

the nasal organs ("Nasenflügelknorpel," SAGEMEHL, 1885; "nasal alar cartilage," KINDRED, 1919). Such a cartilage occurs chiefly in the Cyprinoids and Siluroids, and in the latter group may provide a support for the nasal barbel.

The development and interpretation of the *rostral cartilage*, frequently present in the bony fish chondrocranium, is discussed in the section devoted to the visceral arches.

B. *Ectethmoid cartilages; lateral walls of the ethmoid region.*—Before dealing with the *ectethmoid cartilages* of teleostean fishes it will be convenient to consider the development of the lateral walls of the ethmoid region in *Lepidosteus* and *Amia*.

In a *Lepidosteus* of 14 mm. (VEIT, 1911, p. 57) a short process projecting upwards from the lateral edge of the ethmoid plate marks the commencement of the lateral wall. In a 20-mm. specimen an extensive wall has arisen, which protects the anterior part of the brain, and is said to develop as a dorsal growth of cartilage from the postero-lateral edges of the ethmoid plate. The anterior part of this wall grows inwards and meets that of the opposite side above the brain to form a rudimentary roof, leaving a foramen for the passage of the olfactory nerve; a similar roofing bar is formed by the median fusion of the posterior parts of the lateral walls, and a narrow bar running longitudinally in the fissure between the olfactory lobes connects it with the anterior roof (*t.c.*, p. 78).

In *Amia* the first appearance of the lateral ethmoidal wall takes the form of a short process projecting from the edge of the ethmoid plate as in *Lepidosteus* (cornua parethmoidalia, PEHRSON, 1922, p. 15), which subsequently expands dorsally and fuses with that of the opposite side to form a narrow roofing bar (paraphysial bar, *t.c.*, p. 20). Beyond a certain extension of these processes to form the posterior boundaries of the nasal fossæ, no complete lateral walls comparable to those of *Lepidosteus* are developed in this fish.

In certain Teleosts (notably in members of the order Ostariophysi), in which the chondrocranium is secondarily (?) platybasic and the brain lies on or above the ethmoid plate, a well developed lateral wall projects upwards from near the outer edge of the plate and forms the inner boundary of the nasal fossa. In the remainder, however, owing to the restriction of the anterior extent of the cranial cavity due to the development of an interorbital septum, the lateral ethmoidal walls are even more reduced than in *Amia*, and are in many forms practically non-existent.* Paired ectethmoid cartilages,† similar to those described in *Amia*, are always developed, and provide a boundary between the orbits and the nasal fossæ. With few exceptions (*vide infra*) these elements arise as upgrowths from the postero-lateral edges of the ethmoid plate, as in *Amia* and *Lepidosteus*, but on account of the restriction of the anterior part of the cranial cavity they do not fuse above the brain to form a roofing-bar. Instead, their dorsal ends merge

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* In very young larvæ of *Clupea* the outer edges of the ethmoid plate are turned upwards, and the ethmoid region has the form of a shallow trough. As soon as the brain is withdrawn, however, the plate becomes straightened out.

† "Parethmoid cornua," SWINNERTON, 1902; "antorbital planum," GAUPP, 1906; "parethmoid process," BERRILL, 1925.

either into the hinder part of the mesethmoid cartilage or into the antero-ventral edges of the supraorbital bars, leaving a foramen on each side for the passage of the olfactory nerves (*q.v.*). These ectethmoids may be broad and massive (*Salmo, Cyclopterus*), in which case the olfactory foramen is correspondingly reduced, or they may be represented merely by rods of cartilage as in *Anguilla*.

Gaupp (1906, p. 671) has stated that the ectethmoid cartilages of *Salmo* are pierced by the ophthalmic branches of the trigeminal nerves in their passage to the snout; the small foramen for this ramus is said to lie dorso-lateral to the olfactory foramen. A similar condition is said to occur in *Amiurus* (Kindred, 1919, p. 9). I have studied sections of a 25-mm. Salmon and of young Trout, and find that this nerve runs dorsal and external to the ectethmoid cartilage as it does in *Anguilla* and *Clupea*. There is a small foramen quite close to that for the olfactory nerve, but this serves only as a passage for a small blood-vessel.*

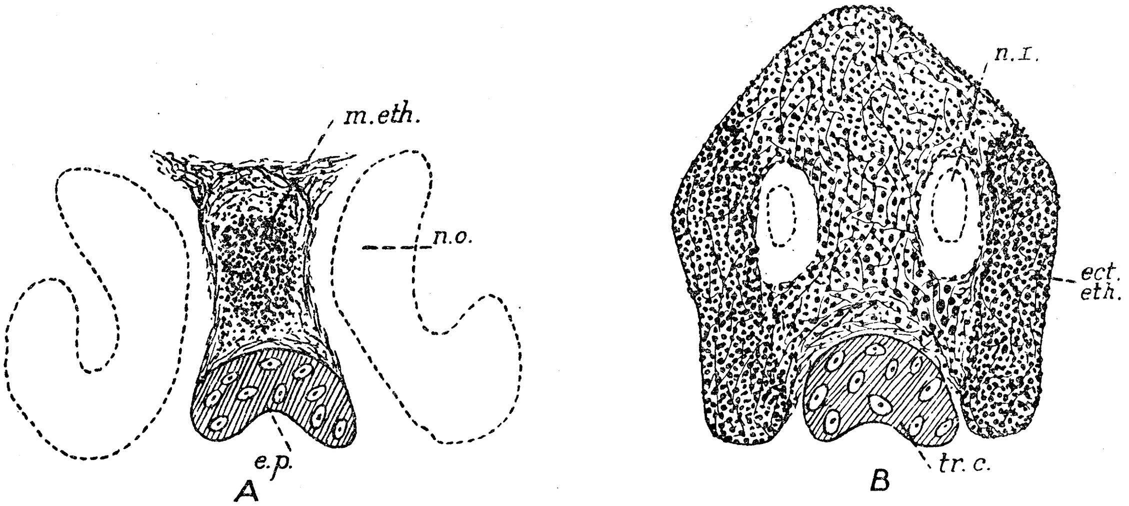

Fig. 40.—Transverse sections of the ethmoid region of an embryo *Siphonostoma typhle*; A, through the middle of the nasal organs; B, through the ectethmoid cartilages, × 200.

Among the few fishes in which the ectethmoids do not arise as outgrowths from the ethmoid plate, *Cyclopterus* and the Syngnathid genera *Syngnathus* and *Siphonostoma* may be mentioned. In *Cyclopterus* these cartilages when first developed are composed of true cartilage above and below but are procartilaginous in the middle. This independent chondrification of the upper ends is clearly a secondary condition (*cf.* Uhlmann, 1921, pp. 281, 299, fig. 3β).

In the Syngnathid fishes† the ectethmoid cartilages arise quite independently of the

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* In a young *Galaxias* examined by me, the ophthalmic ramus of the fifth nerve appears actually to perforate the cartilage.

† Ryder's (1881*b*, pl. XVII) figure of the chondrocranium of a young Sea Horse (*Hippocampus sp.*) shows the mesethmoid and the paired ectethmoid cartilages apparently continuous with the ethmoid plate. Little reliance can be placed on this figure, however, since it was prepared from a whole mount.

ethmoid plate, with which they never become fully connected. The form and development of these elements in *Siphonostoma* may be briefly described.

In early embryos I find a mass of procartilaginous tissue in this region (fig. 40, B), which passes farther forward into the procartilaginous mesethmoid (fig. 40, A). The lateral parts of this mass, corresponding in position to the ectethmoids described by Kindred (1921) in *Syngnathus*,* are more distinctly chondrified than the remainder

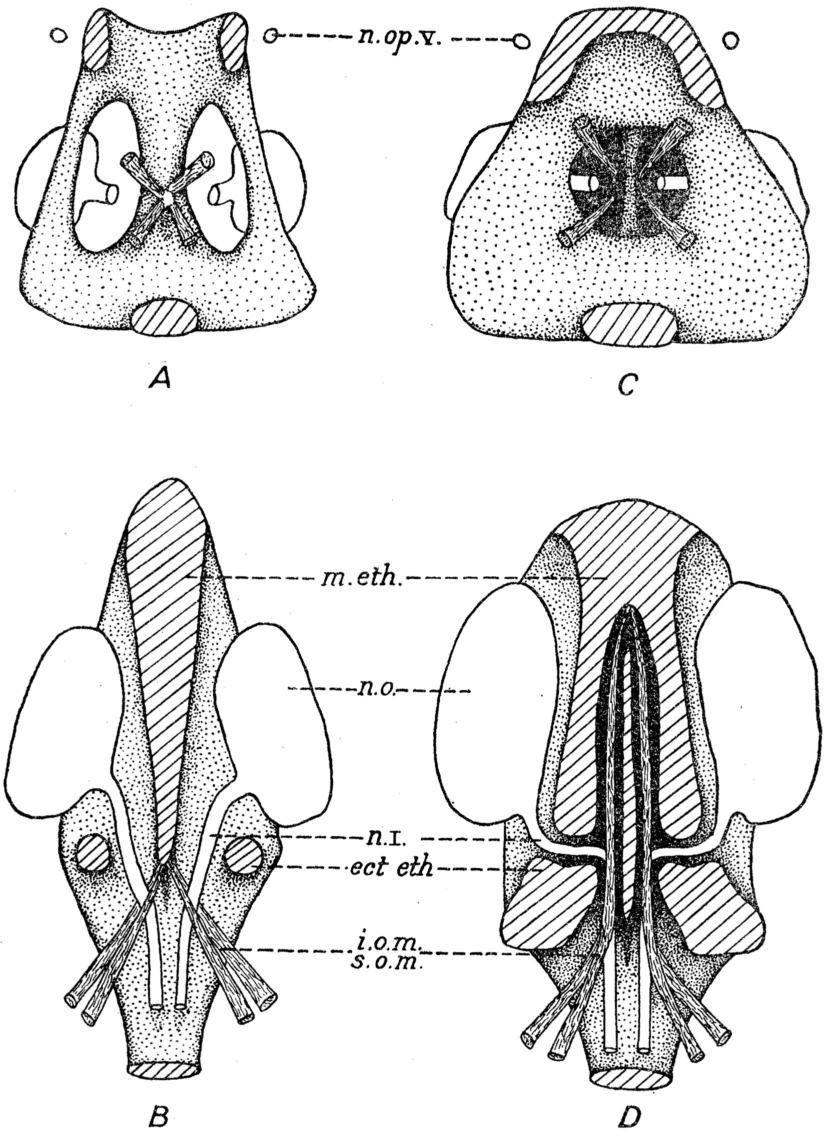

Fig. 41.—Reconstructions of the anterior part of the chondrocranium of A–B, a 31-mm. larva of *Anguilla vulgaris*, C-D, a 25-mm. fry of *Salmo salar*, showing the relations of the oblique eye-muscles and olfactory nerves to the cartilages; × about 110. Figs. A and C represent the anterior regions of the chondrocrania viewed from behind, B and D the lower halves of the same regions viewed from above: the cut surfaces of the cartilages are represented by parallel lines.

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* In a 12-mm. embryo of *Syngnathus*, the two ectethmoids are said to be fused medially to form a narrow bridge, on the dorsal surface of which lies the anterior end of the brain (Kindred, 1921, p. 444).

(fig. 40, B, *ect. eth.*), but are quite unconnected with the ethmoid plate, which is already composed of true cartilage with a definite perichondrium (*e. p.*). Even at an advanced stage these parts are not completely chondrified and are still separated from the plate. KINDRED regards this independence of the ectethmoids as a primitive condition, and concludes that they were derived phylogenetically "from the posterior walls of the cartilaginous olfactory capsules." It seems certain, however, that the ectethmoids of Teleosts are strictly homologous with those of *Amia*, and probably represent the posterior parts of the lateral ethmoidal walls of *Lepidosteus*; their independence of the ethmoid plate in such specialized forms as the Syngnathids seems to be of little importance, and is almost certainly a secondary condition.

The ectethmoid cartilages of the bony fishes seem to be represented in the Selachians (Euselachii) by the expanded cartilaginous wings* which grow outwards on either side from the ethmoid plate and separate the orbits from the nasal organs.† Similar lateral wings have been described in embryos of *Acipenser*, and an examination of PARKER'S (1882*a*) figures of the chondrocranium of this fish leaves little doubt that these wings represent the ectethmoid cartilages of bony fishes. GAUPP (1906, p. 644) has drawn attention to the similarity between the "wing cartilages" of Selachians and the antorbital (ectethmoid) processes of the Urodeles.‡

C. *Relations of the Oblique Eye-Muscles, Olfactory Nerves, etc., to the Chondrocranium.*—In discussing the manner of attachment of the oblique eye-muscles we may divide the chondrocrania of Teleosts into two groups, distinguished respectively by the presence or absence of an anterior eye-muscle canal. The following forms (among others) have a well-developed canal: *Clupea*, *Salmo*, *Galaxias* and *Cyclopterus*. Among those included in the second group, *Cyprinus*, *Amiurus*, *Anguilla*, *Gadus*, *Motella*, *Syngnathus*, *Siphonostoma*, *Scomber*, *Gobius*, *Callionymus*, *Blennius*, *Zoarces*, *Sebastes*, *Gasterosteus*, *Pleuronectes* and *Solea* may be mentioned.

In *Salmo* (fig. 41, C, D) the eye-muscle canal penetrates deeply into the mesethmoid cartilage, and the two pairs of oblique muscles are separated throughout the greater part of the length of the canal by a narrow median septum of cartilage. Both the superior and inferior muscles have their point of attachment at the extreme anterior end of this canal. Just in front of the massive ectethmoid cartilages the olfactory nerves enter the canal from the nasal fossæ, and run through its hinder portion in company with the eye-muscles. This posterior part of the canal is bounded externally by the ectethmoids.

The eye-muscle canal of *Galaxias* is very similar, but no median septum is developed.

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* "Seitliche Fortsätze der Ethmoidal-region," GEGENBAUR, 1872; "Ethmoidalknorpel," SEWERTZOFF, 1897; "laminæ orbitonasales," WIJHE, 1922.

† SEWERTZOFF (1897, p. 414) described these wing cartilages as arising independently in *Squalus* (*Acanthias*). This is incorrect; the elements develop as outgrowths from the ethmoid plate as in *Pristiurus* (SEWERTZOFF, 1899, p. 312) and *Scyliorhinus* (GOODRICH, 1918).

‡ For further notes on the homologies of the ethmoid region of the Selachian skull see :—ALLIS, E. P., "The Homologies of the Ethmoid Region in Selachii," 'Anat. Anz.,' XLIV, 1913, pp. 322–328.

In *Clupea* a common canal, without any septum, lodges the proximal ends of the muscles. In this fish, however, only the superior oblique pair penetrate into the anterior part of the canal, the inferior oblique muscles being attached in the connective tissue surrounding the anterior end of the interorbital septum, at a point about level with the ectethmoid cartilages.

In *Cyclopterus* the muscles of each eye are lodged in independent canals, which are widely separated for their entire length and only penetrate for a very short distance into the basal part of the mesethmoid cartilage (fig. 42). The anterior part of each canal has the form of a groove in the outer edge of the mesethmoid medial to the lateral extension of the ethmoid plate which provides the floor of the nasal fossa (processus antorbitalis, UHLMANN, 1921, p. 286). More posteriorly, where the ectethmoid cartilage connects this lateral ledge with the hinder part of the mesethmoid, the canal has the form of an open groove below the ectethmoid (fig. 42, D).

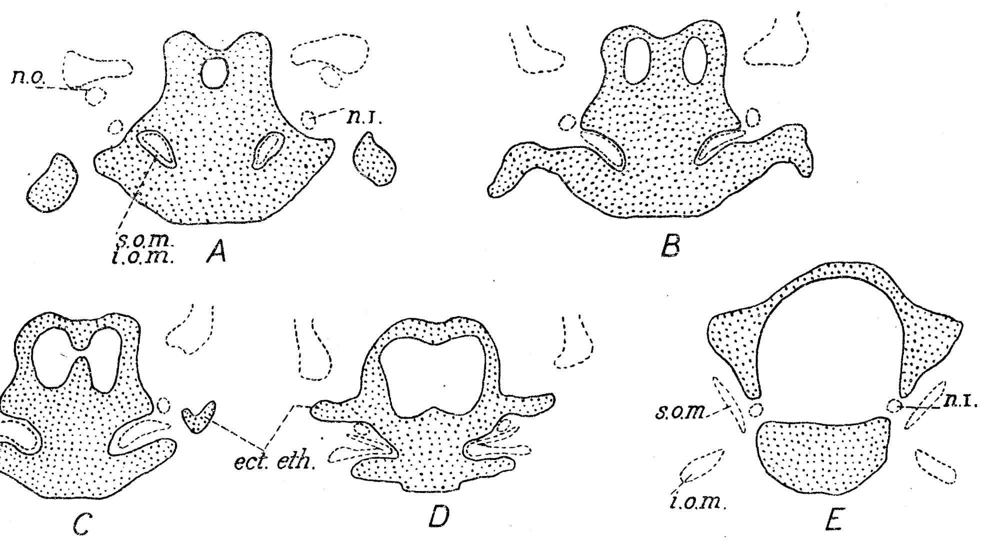

FIG. 42.—A selected series of transverse sections (from before backwards) through the region of the anterior eye-muscle canals in the chondrocranium of a young *Cyclopterus lumpus*, × 38.

Among the Teleosts forming the second group, the oblique eye-muscles of *Syngnathus*, *Siphonostoma*, and *Gobius* have their origin in the fibrous connective tissue surrounding the anterior end of the interorbital septum, at about the middle of its height, and immediately behind the mesethmoid cartilage. The development of a small projection on the posterior edge of the mesethmoid for the attachment of the muscles, which has been described in the larval *Anguilla* (*cf.* fig. 41, A, B) has not been observed in any other fish. In the remaining genera the point of attachment is near the lower end of the septum, and the proximal ends of the muscles are also connected with the dorsal surface of the trabecula communis.

The mode of attachment of the oblique eye-muscles, and the presence or absence of an anterior canal is undoubtedly correlated with the size of the eyes of the *adult* fish.

Thus, in *Salmo* and *Clupea*, which have relatively large eyes this canal, is well developed, whereas it is absent in *Anguilla*, *Amiurus*, etc., in which the eyes are fairly small.

Very short, paired, eye-muscle canals are developed in the larval *Amia*, and the conditions in a 19-mm. specimen are shown in the accompanying figures.* The proximal ends of each pair of muscles have their attachment on the inner wall of a deep groove between the expanded base of the ectethmoid and the low posterior part of the mesethmoid cartilage (fig. 43, C, *s.o.m.*, *i.o.m.*). Below the region where the ectethmoid joins the mesethmoid to form a narrow roof over the groove, the eye-muscles pass outwards into the orbit, and run posteriorly for a short distance in an open niche which forms the anterior corner of the orbit. The inner wall of this niche is the wall bounding the anterior part of the cranial cavity (fig. 43, D). Each eye-muscle canal is continued anteriorly beyond the point of insertion of the muscles, and lodges the olfactory nerve.†

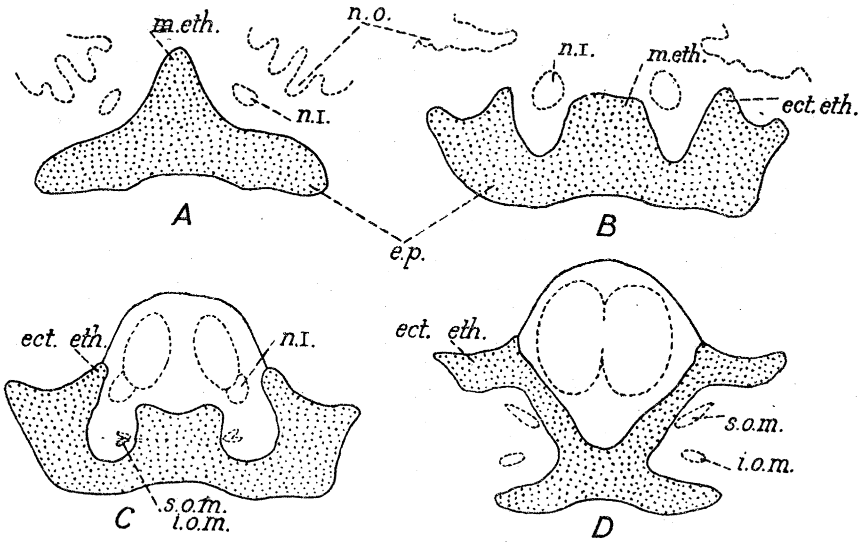

FIG. 43.—A selected series of transverse sections (from before backwards) through the region of the anterior eye-muscle canals of the chondrocranium of a 19-mm. larva of *Amia calva*, × 38.

The elongate eye-muscle canals of *Clupea* and *Salmo* must have been derived from short paired canals similar to those described in *Amia*. The further penetration of these canals into the mesethmoid cartilage, and their subsequent fusion medially would produce the condition found in those Teleosts whose large eyes necessitated a firmer attachment of the related muscles.

No anterior canals are developed in *Lepidosteus*, and the muscles are attached to the inner surfaces of the lateral ethmoidal walls (VEIT, 1911, p. 57).

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* See also — PEHRSON (1922, pp. 19, 21, etc.).

† ALLIS (1897, p. 516, pl. XXV, fig. 25) describes the conditions in the adult fish, and they appear to be very similar to those described in the larva. The muscles penetrate the wall of the elongate olfactory canal which runs forward from the anterior corner of the orbit, and are attached within this canal (*vide infra*).

The paired eye-muscle canals of *Polypterus* have nothing in common with any of those already described. They have been fully investigated by LEHN (1918, p. 388, fig. 16).

The development of the nasal organs, olfactory nerves, etc., and their relation to the cranium in bony fishes has been studied in some detail by SAGEMEHL (1885, 1891); recently, DIETZ* has briefly described these relations in certain Teleosts.

SAGEMEHL recognised three different types of relationship between the anterior part of the brain, the olfactory lobe, and the nasal organ:—(1) "Cyclostome" type—the olfactory lobe lies between the brain and the nasal organ within the cranial cavity, and is closely applied to both; (2) "Selachian" type—the lobe remains in close connection with the nasal organ, but is separated from the fore-brain by a more or less lengthy olfactory tract; (3) "Teleostean" type—the olfactory lobe is enclosed within the brain cavity, the anterior extent of which is restricted by the development of an interorbital septum, and a lengthy olfactory nerve connects the lobe with the nasal organ.

The Cyclostome type never occurs in the adult stage of bony fishes, but it is apparent during the early developmental stages of certain forms (*e.g.*, *Amiurus*,† *Motella*). The Selachian type is characteristic of adult Selachians, members of the teleostean families Mormyridæ and Cyprinidæ, and probably occurs throughout the suborder Siluroidea.‡ The conditions in the Characinidæ appear to be variable, and all degrees of relationship seem to exist between the Selachian and Teleostean types (SAGEMEHL). The olfactory tract, in fishes possessing this type of relationship, lies in a canal which forms an anterior continuation of the brain cavity (fig. 44, A).

The Teleostean type is found in the adult stage of all the remaining Teleosts. The olfactory nerve always leaves the brain cavity in the antero-medial corner of the orbit and enters the nasal fossa through a foramen in the ectethmoid wall, passing in its course freely across the anterior part of the orbit.§

In a 19-mm. larval *Amia* the anterior end of the brain (to which the olfactory lobes are applied) extends forward as far as the ectethmoids, and each olfactory nerve joins the corresponding lobe above the point of insertion of the oblique eye-muscles (*cf.* fig. 43, C). In the adult fish (ALLIS, 1897, p. 513, pl. XXV, fig. 25) the withdrawal of the fore-brain has led to the development of a pair of long olfactory canals, each of which is pierced by a small foramen (orbitonasal foramen, ALLIS) through which the eye-muscles enter the canal. Since this foramen leads directly into the orbit, the olfactory nerve may be

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* DIETZ, P. A., "Über die systematische Stellung der Gadidæ," 'Mitt. Zool. Stat. Neapel,' XXII, 1921, pp. 433–457, 14 figs.

† KINDRED, 1919.

‡ It is also found in the larval stages of a few other Teleosts.

§ GAUPP (1906, p. 586) applies the term "foramen olfactorium evehens" to that foramen through which the olfactory nerve emerges from the brain cavity, and "for. olf. advehens" to that in the ectethmoid wall. In all those Teleosts with an interorbital septum the floor of the anterior part of the brain cavity is membranous, so that the first-named fenestra is not separated by cartilage from the large orbital or optic fenestra.

said to run, for a limited part of its course at least, freely across the orbit as in many teleostean fishes. The relations of the olfactory lobe, brain and nasal organ conform to SAGEMEHL'S Teleostean type, and it is probable that the typical teleostean condition, where the nerve runs freely across the anterior part of the orbit, was derived by progressive fenestration of an olfactory canal similar to that of *Amia*. The development of an interorbital septum, the enlargement of the eyes, and to a lesser extent the penetration of the mesethmoid cartilage by the oblique eye-muscles, would be factors liable to bring about a reduction in the cartilage forming the olfactory canal.

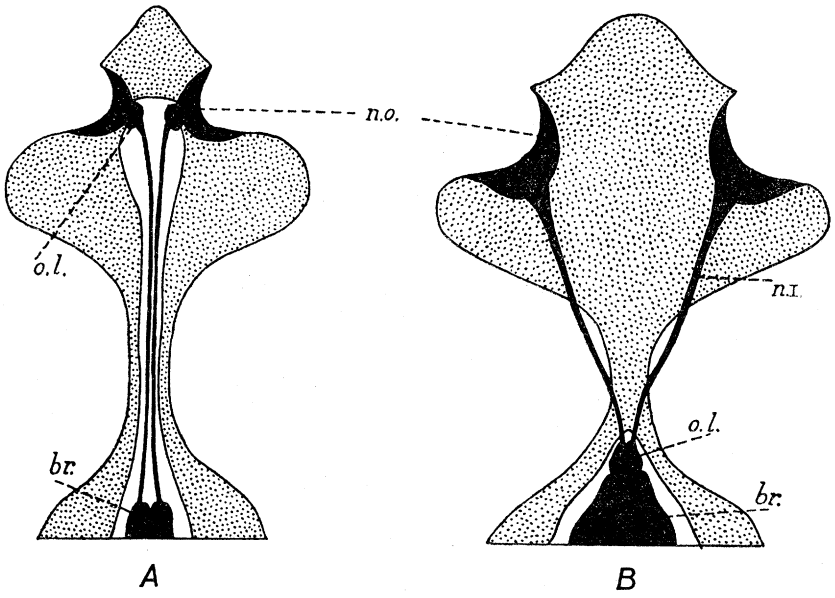

FIG. 44.—Diagrammatic reconstructions of the anterior part of the cranium, showing the relations of the olfactory parts of the nervous system: A, "Selachian" type (*Gadus*), B, Teleostean type: modified from DIETZ.

SAGEMEHL regarded the Teleostean type of relationship as being derived from the Selachian type, but a consideration of the conditions in young and adult *Amia* and *Lepidosteus* leaves little doubt that the teleostean condition represents a direct modification of SAGEMEHL'S Cyclostome type. The conditions found in the Gadidæ and certain other families is clearly a secondary one, the olfactory canal in these fishes having been formed in the upper part of the interorbital septum.

II. *The Orbitotemporal Region.*

A. *Trabeculæ, and their relations with the parachordals; polar cartilages; platybasic and tropibasic types of chondrocranium; basicranial fenestræ, etc.*—In teleostean fishes the *trabeculæ* arise as a pair of independent cartilaginous rods, which either develop in continuity with the parachordal cartilages, or become joined to these elements at an early stage in the ontogeny. SWINNERTON (1902, pp. 511, 560) has shown that the trabeculæ and parachordals may be either continuous or separate in *Gasterosteus*, not only in individuals of the same age, but also on the two sides of the same embryo.

Many authors have laid some stress on the time of appearance of the trabeculæ in relation to that of the parachordals. This point appears to be of little importance, and is confused by the frequent difficulty of ascertaining whether a particular description of the appearance of the trabeculæ or parachordals refers to the actual chondrification of these elements or merely to the first appearance of procartilaginous condensations of cells. Among Teleosts the trabeculæ seem to develop before the parachordals in *Salmo* (STÖHR, 1882, p. 84), whereas in *Sebastes* they are said to be laid down as definite tracts of procartilage at a time when no trace of the parachordals is yet apparent (MACKINTOSH, 1923, p. 503). Among other fishes the trabeculæ appear before the parachordals in *Lepidosiren* and *Protopterus* (AGAR, 1908, p. 50), after them in the Selachians (SEWERTZOFF, 1899, GOODRICH, 1918, WIJHE, 1922) and in *Polypterus*; in *Acipenser* the two elements are said to arise simultaneously (GAUPP, 1906).

In Teleosts the trabeculæ always unite directly with the anterior ends of the parachordals, but in certain other fishes a pair of independent *polar cartilages*[*] at first lie between these two elements, and later fuse with them to complete the chondrocranial floor. These cartilages were first described in *Squalus*[†] (WIJHE, 1905, p. 319; 1922, p. 280), and have been found also in *Lepidosteus*, where they have the form of short rods, and occupy exactly the same position as those of the Selachian fish (VEIT, 1911, p. 28). No independent polar cartilages are developed in *Amia*, but their homologues may be recognised in the broadened, plate-like posterior ends of the trabeculæ (PEHRSON, 1922, p. 3). This homology is further strengthened by the fact that these plate-like expansions bear the same relation to the developing external rectus eye-muscles as do the polar cartilages of *Squalus* and *Lepidosteus*.[‡]

I do not regard these polar cartilages as morphologically independent elements, but rather as parts of the trabecular (or parachordal ?) tracts, which, in certain fishes, have acquired a separate centre of chondrification.[§] Such independent chondrification may be connected with the early development of the rectus muscles and the need for a firm basis for their support.

In connection with the relative positions of the trabeculæ and parachordals, and the manner of their fusion, SEWERTZOFF (1899, p. 316) has introduced the terms

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[*] " Polknorpeln " of German authors.

[†] SEWERTZOFF (1897, 1899) does not mention independent polar cartilages in his description of the early *Squalus* chondrocranium, nor are they developed as separate elements in *Scyliorhinus* (GOODRICH, 1918), or *Heterodontus* (DE BEER, 1924*a*).

[‡] Polar cartilages have been described in a number of higher vertebrates; in Mammals they develop as independent elements, but in birds they are said to be sometimes continuous with the parachordals. They are not present in amphibians.

[§] ALLIS ('J. Anat.,' vol. 58, 1923, pp. 37–51) concludes that the polar cartilages represent the pharyngeal elements of the mandibular arch (*q.v.*), and the trabeculæ the corresponding elements of a præmandibular arch.

"horizontal" and "vertical" to distinguish two types of relationship. In the first type, characteristic of the classes Marsipobranchii and Pisces, and occurring also in some Selachians, the trabeculæ develop more or less in the same plane as the parachordals and fuse directly with the anterior edges of the latter. In the vertical type, found only among the Selachians,* the trabeculæ arise at right angles or almost at right angles to the parachordals, and their dorsal ends subsequently fuse with the *lower* surfaces of the parachordals at some distance behind their anterior ends. Where the trabeculæ fuse with the parachordals in the vertical position, the subsequent straightening out of the cranium produces a well-marked ridge (*sattellehne*, post-clinoid wall) at the junction of the two sets of cartilages, and the presence of such a ridge in the skull of an adult Selachian is regarded as indicating that the relationship of the trabeculæ during development was of the vertical type.†

This subject cannot be discussed at any length here, and it will suffice to point out that the evidence goes to show that the relative positions of the developing trabeculæ and parachordals are influenced mainly by the degree of mesocephalic flexure of the embryonic head.‡ Two explanations of the horizontal and vertical types seem to me probable: (1) that in those fishes possessing the vertical type the flexure is particularly marked; and (2) that the degree of the angle between the two cartilages is correlated with the time at which the flexure appears, or with the time of its maximum development (*i.e.*, in those forms with the vertical type the trabeculæ develop at a time more or less coincident with that at which the cephalic flexure has reached its maximum). The latter explanation appears to be the more probable, since examination of embryos of *Squalus* and *Scyliorhinus* of the same age shows that the degree of flexure is roughly the same in both fishes. Further, in certain Teleosts with a capacious heavily yolked egg, in which the cephalic flexure is well marked,§ the trabeculæ, although bent downwards anteriorly, are certainly of the horizontal type and fuse with the anterior ends of the parachordals.

In considering the later development of the trabecular region of the cranial floor we may distinguish two types of cranium, respectively known as "platybasic" and "tropibasic."|| In the primitive platybasic type the trabeculæ are widely separated throughout the orbitotemporal region, and the brain usually extends well forward into the ethmoid region, and is more or less closely approximated to the floor of the

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* This type has been described in *Squalus* (SEWERTZOFF, 1899, p. 285), *Pristiurus* (t.c., p. 300), *Raia* and *Torpedo* (1897, p. 417), but in *Scyliorhinus* (GOODRICH, 1918) the trabeculæ occupy the horizontal position at all stages; in *Heterodontus* (DE BEER, 1924a, p. 42) the angle is intermediate between that of *Scyliorhinus* and *Squalus*.

† SCHAUINSLAND (1903) figures a well-marked "sattellehne" in an 8·5-mm. embryo of *Callorhynchus* (Holocephali).

‡ SWINNERTON (1902, p. 560) has reviewed this question at some length.

§ KERR ("A Treatise on Comparative Embryology," II, London, 1919, p. 94) suggests that the degree of mesocephalic flexture is dependent on the amount of yolk present in the egg.

|| "Platytrabic" and "tropitrabic," WIJHE (1922, p. 284).

cranium. This type is characteristic of most Selachians, and occurs also in *Acipenser*, *Polypterus*, *Amia* and *Lepidosteus*[*] ; among Teleosts it is found only in the Siluroidea, and in *Homaloptera* among the Cyprinoidea (SAGEMEHL, 1891).[†] In all the remaining Teleosts the cranium is tropibasic in the adult at least, but may pass through a distinctly platybasic stage during the early part of its development.

The tropibasic type is distinguished by the fusion of the trabeculæ in front of the hypophysis to form a median bar of cartilage—the *trabecula communis,* which is surmounted by a membranous or cartilaginous interorbital septum (*q.v.*) limiting the anterior and ventral extent of the brain cavity. In some of the more specialised Teleosts (*e.g.*, the Syngnathidæ, *Sebastes*) the trabeculæ are approximated at a very early stage, or may even arise as a single procartilaginous tract.

The formation of the trabecula communis in *Clupea* occurs at a comparatively late stage in the ontogeny, and may be briefly described. In the early stages (larvæ of 5 to 20 mm.) the trabeculæ are widely separated, and, although cartilage is developed between their anterior ends during this period, no trabecula communis or interorbital septum is apparent. In a 30-mm. larva the greater part of these cartilages have been absorbed, and the cranial floor in this region is represented by a posteriorly directed process projecting from the middle of the ethmoid plate. This process represents the remains of a plate which was formed by the development of cartilage between the anterior ends of the paired trabeculæ. It has the form of a typical trabecula communis, and is surmounted by a low but definite membranous interorbital septum. In a 40-mm. larva this septum is considerably higher, and the extent of the brain cavity is correspondingly diminished. The trabecula communis of *Clupea* thus differs in the manner of its formation from that of other Teleosts, where it arises through a simple fusion of the paired trabeculæ.

In all fishes one or more fenestræ are present in the floor of the chondrocranium, and these may or may not be closed by development of cartilage or bone at a later stage. The form and extent of the fenestra or fenestræ differ considerably in various fishes.[‡] In the platybasic cranium of bony fishes there is always a single large basicranial fenestra[§] into which the anterior end of the notochord at first projects. This may be somewhat narrowed in the middle, so that anterior and posterior sections are to be recognised (*Amia, Lepidosteus*). A similar and homologous basicranial fenestra is present during the early stages in the Selachian chondrocranium.[||] In the Selachians the fenestra is subsequently entirely closed by growth of cartilage ; in the adult *Lepidosteus* it is

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[*] At least during the early developmental stages and probably also in the adult.

[†] The condition is probably secondary in these fishes.

[‡] In discussing the fenestræ in the cranial floor I have entirely omitted the fissure between the parachordals, which is entirely filled by the intercranial notochord.

[§] In describing the single fenestra in the chondrocranium of *Amiurus,* KINDRED (1919) applies the term "fenestra hypophyseos" to the anterior part, and "fenestra basicranii anterior" to the hinder portion.

[||] "Intertrabecular basal fontanelle," SEWERTZOFF (1899) ; "polar fenestra," WIJHE (1922).

reduced to very small proportions; and in *Amia* and *Acipenser* it is almost entirely closed by cartilage. In the adult *Polypterus*, however, it is scarcely reduced.

In the tropibasic cranium the united trabeculæ always diverge in the region of the hypophysis to enclose a fenestra, which extends backwards between the anterior parachordals, and into which the tip of the notochord projects during the early stages of development.* The widening of the bordering cartilages in the middle of this fenestra may divide it into anterior and posterior sections (*Salmo*, *Gasterosteus*), but in most Teleosts such a division is scarcely indicated. A splitting off of a part of the original fenestra to form a carotid foramen, such as occurs in *Anguilla*, has not been described in any other bony fish. The basicranial fenestra of the teleostean chondrocranium is never closed by growth of cartilage, but may be somewhat reduced in size during the ontogeny; it is finally more or less completely closed by the development of the parasphenoid bone.

The development of the infundibulum and hypophysis, by inhibiting the growth of cartilage in this region, is undoubtedly the primary cause of the presence of a basicranial fenestra, but the relative positions of fenestra and hypophysis vary greatly in different fishes, and also undergo some change during the ontogeny.† For this reason many of the terms which have been employed to denote the fenestra or parts of the fenestra in Teleosts, most of which refer to its position relative to the hypophysis, are unsuitable.‡

B. *Relations of the carotid and other arteries to the base of the chondrocranium, and the formation of carotid foramina; attachment of the posterior eye-muscles, and the formation of a myodome.*—The development of the principal cranial arteries, and their relations to the cartilages in different fishes, have been dealt with in detail by De Beer (1924*b*). In this paper I propose chiefly to compare the conditions found in the larval *Anguilla* with those pertaining in other Teleosts. Many of the published accounts of the

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* Mackintosh (1923, p. 506) states that "there is no sign of a fenestra hypophyseos" in the chondrocranium of a 5·5-mm. *Sebastes*, but examination of his preparations shows that this is incorrect.

† The change in the relative positions of the fenestra and hypophysis during the development of *Anguilla* has been already described. I find a similar change of position in *Clupea*, and, to a lesser extent, in *Siphonostoma*.

‡ Where a single undivided fenestra is present, the following names have been used:—"Pituitary space," Parker, 1873; "pituitary foramen," Wells, 1923; "fenestra hypophyseos," Uhlmann, 1921, and others: where the fenestra is divisible into anterior and posterior sections, the terms "fenestra hypophyseos," "fenestra basicranialis anterior" (Gaupp, 1906), and "pituitary fossa" (Swinnerton, 1902) have been applied to the first, and the hinder portion has been designated "fenestra basicranialis posterior" (Gaupp, 1906) or "interparachordal fossa" (Swinnerton, 1902). In describing the single slit-like fenestra of *Syngnathus*, Kindred employed the terms "fenestra myodomus ventralis," "fenestra hypophyseos," and "fenestra basicranii posterior" for its anterior, middle and posterior sections respectively.

Where a single fenestra is present the term "*basicranial fenestra*" may be suitably employed, and if it is necessary to distinguish two sections these may be called the "*anterior basicranial fenestra*" and "*posterior basicranial fenestra*" respectively. The fissure between the parachordals occupied by the notochord may be conveniently designated the "*interparachordal*" or "*notochordal fissure.*"

teleostean chondrocranium contain little or no details of the arrangement of the arteries, and for this reason I have found it necessary to study an extensive series of larval fishes in order to obtain a clear idea of the relations in different genera.

The fusion of the internal carotid arteries in the *Leptocephalus* larva to form a median trunk, which also receives the efferent pseudo-branchial arteries (mandibular vessels), represents an unusual condition and appears to be unique among larval and embryo Teleosts. In *Syngnathus* and *Siphonostoma* the internal carotids are closely approximated within the cranium, a condition which is found in several other forms, but no actual fusion takes place. HOCHSTETTER* (p. 93) states that these arteries are at first independent in all Teleosts, but later become connected by a cross-commissure. According to ALLIS,† who has studied their relations in a number of forms, this condition is found in many adult Teleosts, although in others the internal carotids are fused as in the larval *Anguilla*. No such transverse commissure is apparent in the majority of the forms examined by me, but I find it in fairly advanced larvæ of *Clupea*, *Sebastes* and *Gobius*, where it lies anterior to the hypophysis and within the cranium.

ALLIS (1919, p. 277) concludes that the fusion of the internal carotids in Teleosts is due to a pressure exerted by the muscles of the eyeball, but this cannot be so in *Anguilla*, since here the eye muscles are well separated from the arteries, with which they are in no way connected. The approximation of the two vessels in the Syngnathidæ is undoubtedly due merely to the compression of the whole head, and the extreme lateral flattening of the head of *Leptocephalus* would seem to be the cause of their fusion in that fish.

The arrangement of the principal cranial arteries in a 28-mm. embryo of *Squalus* (WIJHE, 1922, p. 281) somewhat resembles that of the larval *Anguilla*. The internal carotids pass upwards through the basicranial fenestra (polfenster), and unite to form a median vessel which divides anteriorly into two branches ; each branch runs outwards in front of the polar cartilage and joins the efferent pseudo-branchial artery (carotis spiracularis), which near this point gives off a branch to the eye-ball. In the Selachians, however, the efferent pseudo-branchial vessel always passes *above* the trabecula to join the carotid, but in all other fishes,‡ as well as in the higher vertebrates, it runs below the trabecula. The condition in Selachians is without doubt a secondary one. In adult Selachians the internal carotids may be fused medially or connected by a transverse commissure (ALLIS, 1919, p. 277).

In all Teleosts with a tropibasic chondrocranium examined by me the internal carotids

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* HOCHSTETTER, —., "Die Entwicklung der Blutgefässsystems," in Hertwig's 'Handbuch d. vergl. u. experim. Entwick. d. Wirbeltiere,' Jena, 1906, No. IV (Bd. III (2), pp. 21–166).

† ALLIS, E. P., "The pseudobranchial and carotid arteries in *Ameiurus*," 'Anat. Anz.,' vol. 23, 1908, pp. 256–270, 1 fig., "The pseudobranchial and carotid arteries in *Esox*, *Salmo* and *Gadus*, together with a description of the arteries in the adult *Amia*," 'Anat. Anz.,' vol. 41, 1912, pp. 113–142, 6 figs., "The pseudobranchial and carotid arteries in the Gnathostome fishes," 'Zool. Jahrb.,' 'Abt. Anat.,' vol. 27, 1909, pp. 103–134, pl. IX, and other papers by the same author.

‡ Except *Amiurus* (?)—KINDRED, 1919.

enter the cranium through the basicranial fenestra, and no distinct carotid foramen, comparable to that described in the larval *Anguilla*, is developed.

In *Amia* and *Lepidosteus* paired carotid foramina are present in the chondrocranium, and eventually occupy a position antero-lateral to the reduced basicranial fenestra. The formation of these foramina in *Amia* (Pehrson, 1922) takes place in the following manner : each internal carotid at first enters the cranial cavity through a notch between the trabecula and the expanded polar plate ; subsequently a process grows out anteriorly from the plate, and, fusing with the trabecula, converts the notch into a carotid foramen. Clearly, the single foramen of *Anguilla* cannot have been derived from the fusion of such paired foramina, and must have been acquired independently.

The similarity in the arrangement of the arteries in the larval *Anguilla* and embryo *Squalus* has been already mentioned, and it is interesting to note that in both fishes the single carotid foramen also arises in the same manner. In a 28-mm. *Squalus* (Wijhe, 1922) the internal carotids pass upwards through the basicranial fenestra, and in a specimen of 39·5 mm. the hinder part of this fenestra has been separated off to form a carotid foramen which already occupies approximately the same position as in the adult fish (Wells,* p. 424, Pl. I, fig. 2c).†

The manner of attachment of the posterior eye-muscles in the larval *Anguilla* has been fully described in the first part of this paper, and we may now examine the conditions in other Teleosts.‡ Considering only the chondrocranium of larval and young forms, two distinct types of attachment may be recognised : (1) where the muscles are attached within the cranium, none of them passing through the basicranial fenestra ; (2) where certain of the muscles penetrate this fenestra, run in a posterior direction below the cranial floor, and have their attachment external to the cartilaginous cranium—*i.e.*, where a posterior eye-muscle canal or myodome is developed. In describing the attachment of the anterior eye-muscles I have shown that the presence of an anterior muscle canal is correlated with the possession of large eyes by the adult fish. The same is generally true for the posterior myodome, but it must be noted that *Gasterosteus* has a well-developed posterior canal, but the oblique (anterior) muscles are merely inserted in the tissue surrounding the interorbital septum.

Anguilla may be taken as a typical example of the first type of attachment, which also occurs in a large number of other Teleosts. In nearly all these fishes some of the

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* Wells, G. A., " The Skull of *Acanthias vulgaris*," ' J. Morph.,' XXVIII, 1917, pp. 417–436, 3 pls.

† Allis (1919) studied the conditions in adult fishes and concluded that the carotid foramina of *Amia* and the Selachians were not homologous. This is fully confirmed by an investigation of the manner of their development.

‡ Klein (" Beiträge zur Bildung des Schädel der Knochenfische," ' Jahresheft des Vereins f. Vater Naturkunde, Wurttemberg,' XL, 1884, pp. 129–255) has published lists of those Teleosts with and without a functional myodome, and these lists have been supplemented by Starks (" Some Notes on the Myodome of the Fish Cranium," ' Science,' XXI, 1905, pp. 754–755), and Allis (1919). The latter author has dealt with the structure and homologies of the myodome in several adult and young Teleosts in great detail.

rectus muscles run, for a short distance at least, between the base of the brain cavity and the cartilaginous floor of the cranium, thus occupying a rudimentary myodome, but none of these muscles pass through the basicranial fenestra or have their attachment outside the chondrocranium.*

I have studied the posterior eye-muscle canal in a 25-mm. specimen of *Salmo salar*,† and in a series of larvæ of *Clupea harengus*,‡ and propose to describe the conditions in these two Teleosts which may be taken as representing the group of forms with a well-developed canal and comparatively large eyes.

In the first or anterior section of the canal of *Salmo,* which is situated entirely in the orbitotemporal region, the floor is formed by the trabeculæ and a transverse membrane stretched between them over the basicranial fenestra, the roof by the membranous base of the brain cavity, and the lateral walls by the ventral parts of the postorbital cartilages. In the middle section, lying partly in the orbitotemporal region and partly in the auditory region, the floor is formed by the anterior parachordals, the medial parts of which become depressed during development owing to the pressure of the external rectus muscles ; the roof is similar to that of the anterior section, and the lateral walls are formed by the anterior basicapsular commissures joining the auditory capsules and parachordals.§ The posterior section of the myodome, situated wholly outside the chondrocranium, communicates with the middle section through the basicranial fenestra. The roof of this part is formed by the chondrocranial floor (*i.e.*, by the parachordals), the floor by the parasphenoid bone, and the lateral walls by a pair of longitudinal cartilaginous ridges developed on the ventral surface of the parachordal plate. According to GAUPP (1906) the rectus muscles pass through the basicranial fenestra during the ontogeny, and penetrate posteriorly between the cranial floor and the developing parasphenoid lamella ; the subsequent thickening of the muscles forces the bone away from the parachordal plate.||

In a 10-mm. larva of *Clupea* certain of the rectus muscles have already passed outwards through the basicranial fenestra, and appear to be inserted on the ventral surface

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* In the Syngnathidæ the proximal ends of the rectus eye-muscles are inserted on the parasphenoid bone immediately below the basicranial fenestra.

† For further notes on the form and development of the myodome in *Salmo*, see SCHLEIP (1904, pp. 355–359—*S. trutta*) and GAUPP (1906, pp. 665–669—*S. salar*). PARKER (1873, p. 102, pl. VIII, fig. 2) describes and figures the hinder section of the canal, without, however, comprehending its significance.

‡ WELLS (1923) does not mention the extensive myodome in his description of the chondrocranium of *Clupea*.

§ At a later stage cartilage appears in the membranous roof of this section, expands anteriorly and posteriorly, and finally forms a bridge (" prootic bridge," ALLIS, 1919) extending between the lateral edges of the anterior parachordals which were not involved in the depression undergone by the more medial regions (GAUPP, 1906).

|| In *Pleuronectes* and *Solea* the posterior part of the canal is formed at a comparatively late stage, and the eye-muscles grow backwards in the canal left by the receding tip of the notochord (BERRILL, 1925, p. 223).

of the parachordals, at a point a little behind the tip of the notochord. A slight depression of the anterior parts of the parachordals is already apparent; during the later stages this is increased, and is accompanied by a similar, but less marked depression of the posterior ends of the trabeculæ. In a 20-mm. specimen (fig. 45, A–C) the external and internal rectus muscles extend almost as far as the occipital region, and posteriorly they occupy a shallow groove in the ventral surface of the parachordal plate (fig. 45, C).

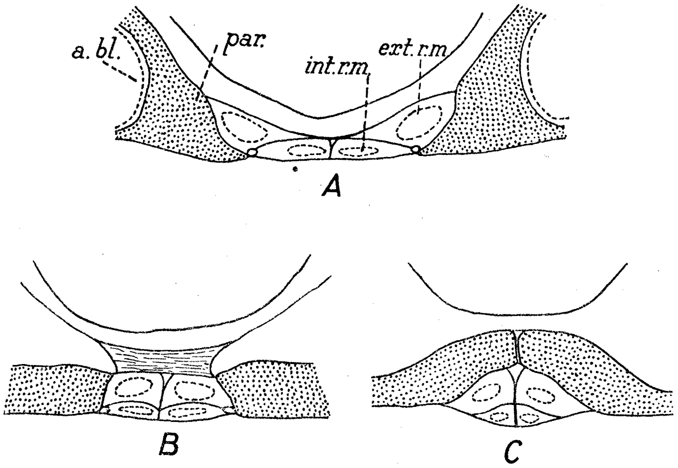

FIG. 45.—A selected series of transverse sections through the region of the myodome in the chondrocranium of a 20-mm. larva of *Clupea harengus*, × 73.

In a 30-mm. larva (fig. 46, A–E), cartilage has appeared in the membranous roof of the middle section of the myodome as in *Salmo*, and the posterior part is now represented by a deep groove in the parachordal plate, which is closed ventrally by the parasphenoid bone. The lateral walls of this part do not appear to have been formed mainly by downgrowths of cartilage from the parachordals as in *Salmo*, but the muscles have actually penetrated into the substance of the cartilaginous cranial floor. The middle and posterior sections of this myodome are divided by a vertical membranous partition, and each of the compartments thus formed is further divided by a horizontal membrane into dorsal and ventral sections.*

The form and development of the myodome in *Gasterosteus* (SWINNERTON, 1902, pp. 518, 527) is exactly similar to that of *Salmo*.

The point of attachment of the superior and inferior rectus muscles is always anterior to that of the external and internal pairs, and these muscles are inserted on the vertical median partition in the anterior section of the myodome. This membranous partition forms a posterior continuation of the interorbital septum. In *Salmo* the internal rectus muscles are inserted in the middle section of the canal, and the external pair in the hinder part; in *Clupea* both sets of muscles pass out into the extracranial section and are inserted at the extreme hinder end of the cranium.

The myodome of teleostean fishes would appear to have arisen in the following manner.

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* A part of this horizontal myodomic membrane may chondrify or ossify in certain Teleosts.

The rectus muscles, which were probably at first attached to the external surface of the cranium, have at some time forced their way inside the cranium, pushing the base of the brain cavity dorsally. It is probable that in this migration they occupied præ-existing lymph spaces or canals, rather than forcing their way through solid cartilage and connective tissue. In this way the anterior and middle sections of the myodome would be formed. In certain fishes one or two of the pairs of rectus muscles, in order to obtain a firmer attachment, have grown out posteriorly through the basicranial fenestra, and have either pushed backwards between the parachordal plate and parasphenoid bone, or have occupied some canal previously occupied by blood or lymph vessels.* No part of the myodome appears to be a derivative of the cranial cavity as suggested by SWINNERTON (1902, p. 528).

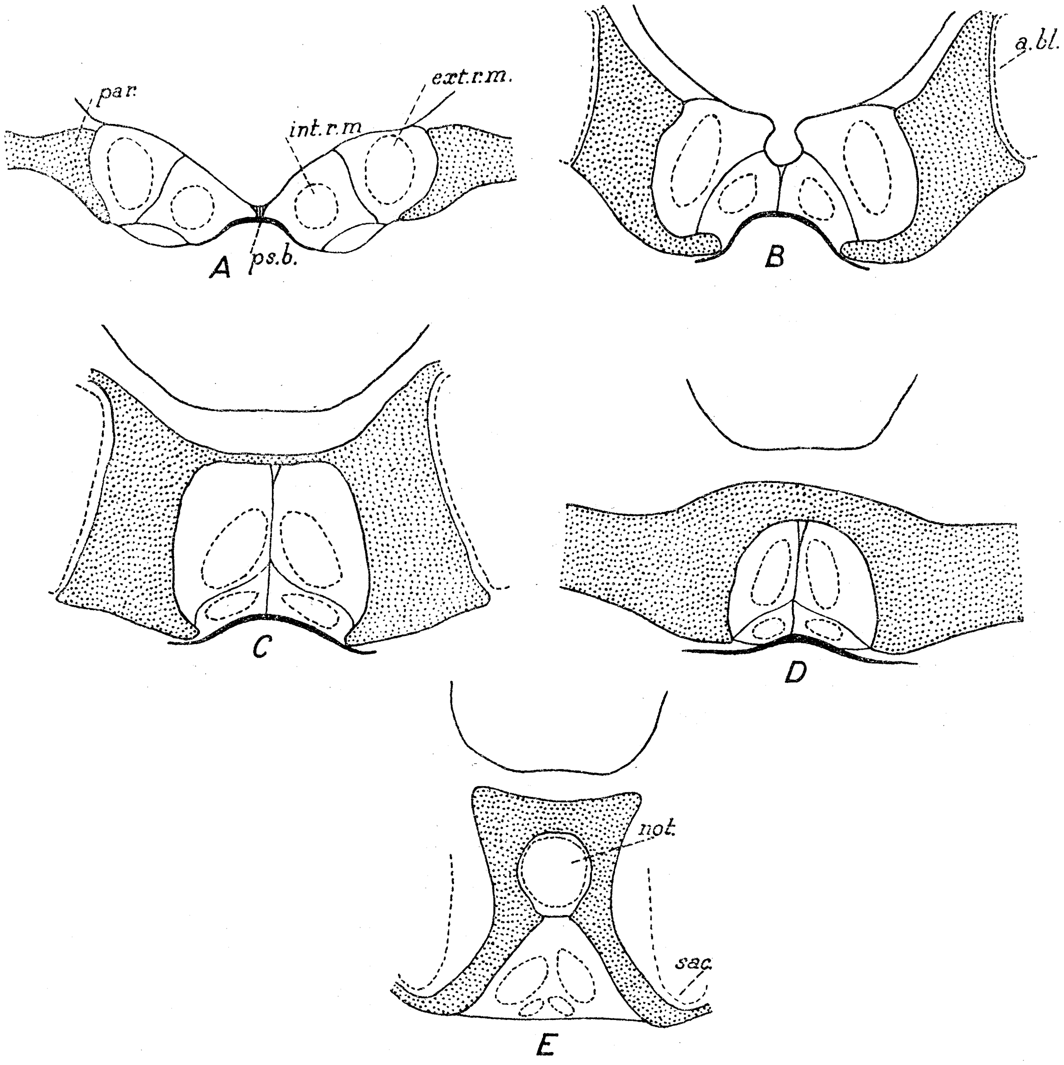

FIG. 46.—A selected series of transverse sections through the region of the myodome of a 30-mm. larva of *Clupea harengus*, × 73.

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* See ALLIS (1919) for a discussion of this question.

C. *The lateral walls of the orbitotemporal region ; supraorbital bars ; interorbital septum.* —In the tropibasic chondrocranium of Teleosts the lateral walls of this region are reduced to a pair of more or less narrow bars of cartilage—the *supraorbital bars*,* which lie between the brain and the upper parts of the eyes, and form the dorsal boundaries of the large optic fenestræ. In *Clupea, Salmo, Anguilla* and most other Teleosts, these bars become completed at some stage of development, and extend from the ethmoid region to the anterior edges of the auditory capsules; in some of the more specialized forms, however (*e.g., Gasterosteus, Sebastes* (?))† they may remain incomplete. In the Syngnathidæ they are practically non-existent, their anterior and posterior ends being represented by short processes projecting from the ectethmoids and auditory capsules respectively.

Just anterior to the capsules, in the region of the trigemino-facialis complex, the lateral walls of the teleostean chondrocranium are generally complete. These postorbital walls will be discussed further in connection with the auditory region.

In a number of genera the paired supraorbital bars are connected with one another by a transverse bridge of cartilage lying behind the epiphysis (*epiphysial bar*), and cartilage may also be developed between their anterior ends to form a rudimentary cranial roof (*q.v.*).

In the platybasic chondrocranium the lateral walls are generally formed by extensive plates of cartilage ("Alisphenoid cartilages," KINDRED, 1919), which may be fused ventrally to a greater or lesser extent with the trabeculæ, thus restricting the size of the optic fenestræ.‡ The manner in which these lateral plates are developed has not been described.

Before dealing with the lateral walls of the orbitotemporal region in Ganoids and Selachians, it will be convenient to consider the development of the supraorbital bars in those Teleosts with a tropibasic chondrocranium, and particularly in the more primitive genera (*e.g., Clupea, Salmo*, etc.). Since the epiphysial bar is intimately connected with the supraorbital bars, the development of both cartilages may be considered together.

In *Clupea* each bar arises as an outgrowth from the anterior edge of the auditory capsule, and eventually joins the rudimentary anterior cranial roof. In a 10-mm. larva the bars are still incomplete, but they are already connected by a transverse epiphysial bar. The manner in which the supraorbital bars arise in *Salmo* has not been clearly described, but GAUPP'S account of the chondrocranium suggests that they develop as in *Clupea*.§ The presence of a suture between the hinder end of each supra-

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* "Tæniæ marginales," GAUPP, 1906; "postorbital processes," WELLS, 1923.

† The series of stages examined by MACKINTOSH (1923) was incomplete.

‡ In *Gymnarchus* the lateral walls are almost complete in a forty-third day larva, and the optic fenestræ are reduced to minute proportions (ASSHETON, 1907, p. 407, figs.).

§ RUTHERFORD (1909, p. 691) describes a pair of independent cartilages on either side of the orbito-temporal region in a young Trout, but this is not confirmed by other workers.

orbital bar and the cartilage of the auditory capsule in the youngest *Leptocephalus* larva examined by me suggests that in this fish the bars do not grow out from the capsules as in *Salmo* and *Clupea*.

Among other Teleosts in which a complete series of stages has been studied, the supraorbital bars in *Pleuronectes* and *Solea* (BERRILL, 1925, pp. 225, 227) arise exactly as in *Salmo* and *Clupea*. In *Cyclopterus* (UHLMANN, 1921) and *Gasterosteus* (SWINNERTON, 1902) the epiphysial bar arises first as a pair of independent cartilages situated on either side of the brain, which soon unite medially to complete the transverse bar. In *Cyclopterus* each of the original epiphysial cartilages becomes connected anteriorly with the ectethmoid (tænia antorbitalis) and posteriorly with a process growing forward from the auditory capsule (tænia postorbitalis); in this manner the supraorbital bars are completed. In *Gasterosteus* similar connections are established between ectethmoids and epiphysial bar, but, although processes grow forward from the capsules, these never join the epiphysial bar.

In *Lepidosteus* the lateral walls of the orbitotemporal region during the larval stages are represented by supraorbital bars* which may be homologous with those of *Clupea* and *Salmo*, and appear to develop in the same manner (VEIT, 1911).

In *Amia* the first trace of the lateral walls is apparent in a $10\frac{1}{2}$-mm. larva, in which a pair of small, independent cartilages arise between the eyes and the mesencephalon (PEHRSON, 1922, p. 18—" supraorbital cartilages "). In a 12-mm. larva the framing of the orbit is complete, and this has been accomplished in the following manner: each ectethmoid has grown backwards to join the supraorbital cartilage, which has itself extended posteriorly to fuse with the anterior edge of the auditory capsule. The epiphysial bar arises at this stage from a pair of cartilages which are quite independent of the supraorbital bars, with which they are perichondrially connected.†

In Selachian fishes the lateral walls of the orbitotemporal region arise as a pair of primarily independent *sphenolateral cartilages*.‡ WIJHE (1904, 1922) has described another pair of independent cartilages (" supraorbitals ") in *Squalus* and *Raia*, which latter fuse ventrally with the sphenolaterals and anteriorly with the orbitonasal plate; these supraorbitals do not appear to have been recognised in any other genera. The sphenolateral cartilages soon expand and become fused postero-ventrally with the

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* VEIT (1911) does not make it clear whether these cartilages arise independently, but his figures would suggest that they grow out from the auditory capsules.

† Attempts have been made to compare the processes of development of the supraorbital bars of *Cyclopterus* with those of *Amia*. In *Amia*, however, the posterior parts of these bars arise by the posterior growth of the independent supraorbital cartilages, whereas in *Cyclopterus* they are formed by outgrowths from the capsules.

‡ " Alisphenoid," SEWERTZOFF, 1897—*Squalus, Pristiurus*, etc.; " lamina antotica," WIJHE, 1904—*Squalus*; GOODRICH, 1918—*Scyliorhinus*; " pleurosphenoid," GAUPP, 1906; " sphenolateral," WIJHE, 1922—*Squalus*; DE BEER, 1924*a*—*Heterodontus*.

Wijhe's term " sphenolateral " appears preferable to " alisphenoid," since the homology of these cartilages with the alisphenoids of higher craniata is as yet uncertain.

anterior parachordals; their subsequent junction with the anterior margins of the auditory capsules completes a foramen for the trigeminal, facial, and abducens nerves (prootic foramen). At a comparatively late stage in the ontogeny, each sphenolateral grows out anteriorly and fuses with the lateral ethmoid wing (= ectethmoid cartilage), at the same time becoming joined to the trabecula ventrally and thus completing the lateral wall of the orbitotemporal region.

The manner of the formation of the posterior portions of the supraorbital bars of *Amia* (*i.e.*, those parts behind the epiphysial bar) appears to be more primitive than that of the same cartilages in *Clupea* and *Salmo*. The supraorbital cartilages of PEHRSON'S (1921) description of the chondrocranium correspond to the sphenolateral cartilages of Selachians or at least with their dorsal parts, the ventral extent of the lateral walls in this region being reduced, partly owing to the enlargement of the orbits and partly on account of the replacement functionally of the cartilaginous walls by bones. The independent origin of the epiphysial cartilages in *Cyclopterus* and *Gasterosteus* seems to me to be a secondary condition and of little importance.* The more extensive lateral walls (alisphenoids) of the platybasic teleostean chondrocranium appear to have been secondarily derived by the ventral expansion of the supraorbital bars, and are probably in no way homologous with the sphenolaterals of Selachians.

The *interorbital septum*, a characteristic feature of the tropibasic cranium, appears to be confined to the teleostean fishes.† As far as the larval chondrocranium is concerned, the development of a trabecula communis is not always accompanied by the formation of a septum, although this is generally the case. In *Motella*, *Gobius*, and *Cyclopterus* the trabeculæ are united at an early stage, but a septum is scarcely apparent between the eyes, and the brain cavity extends downwards almost as far as the chondrocranial floor. In many genera, owing to the great enlargement of the eyes, the trabecula communis comes to lie between their lower halves (*Anguilla*) or even level with their middle parts (*Siphonostoma*, *Gadus*, *Gobius*, *Cyclopterus*, etc.); thus, the interorbital septum may separate only the upper parts of the eyes.

When the interorbital septum first arises it is always low throughout its length, and becomes progressively higher as development proceeds. It is invariably highest between the anterior parts of the eyes, becoming lower as it approaches the basicranial fenestra, where the brain cavity lies correspondingly closer to the cranial base.‡ Its extreme hinder portion lies between the rectus eye-muscles, and, in those forms in which a

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* POLLARD ("On the Anatomy and Phylogenetic Position of *Polypterus*," 'Zool. Jahrb.,' V, 1892, 'Abt. Anat.,' pp. 387–428, 10 figs.) has compared the supraorbital bars of Teleosts with the later developed ridges above the orbits in the Selachian cranium.

† VEIT (1907, p. 19, fig. 12) describes a so-called cartilaginous interorbital septum in the adult *Lepidosteus*, but this is merely the hinder part of the mesethmoid cartilage which projects a little into the orbital region.

‡ In a 25-mm. *Salmo*, GAUPP (1906, p. 668) distinguishes three sections of the interorbital septum: an anterior, high "prochiasmatic" region, and, more posteriorly, low "hypochiasmatic" and "metachiasmatic" parts.

myodome is developed, the septum is continued into the anterior part of this canal as the vertical myodomic membrane.

In the larval and post-larval chondrocranium the septum is nearly always composed chiefly of membranous tissue, consisting of a fine membrane during the early stages and becoming progressively thicker during development. In certain forms, however, the lower part of its anterior section becomes cartilaginous. In a young *Zoarces* (fig. 47, A) this part of the septum arises through the dorsal growth of a thin plate of cartilage from the trabecula communis. Similar conditions are found in *Blennius* (fig. 47, C) and *Sebastes* (fig. 47, B). In certain Teleosts (*e.g.*, *Gadus*) the interorbital septum becomes completely ossified at a later stage. The septum is always attached dorsally to the membranous base of the brain cavity, and ventrally to the trabecula communis or to the membrane stretched between the diverging posterior ends of the trabeculæ. In *Salmo* the trabecula communis is said to grow out into a dorsally directed comb of cartilage to which the septum is joined, but in *Anguilla*, and in many other genera, it is attached merely to the perichondrium of this cartilage.

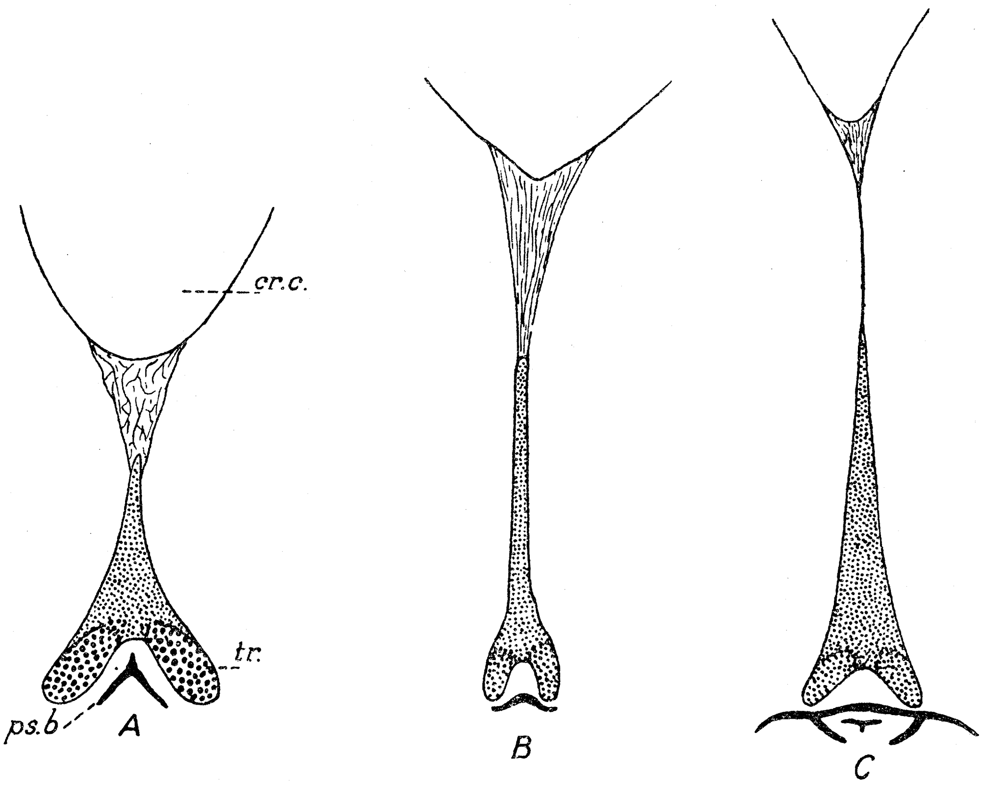

Fig. 47.—Transverse sections through the anterior region of the interorbital septum in A, a 25-mm. *Zoarces viviparus*, × 100 ; B, a 25-mm. *Sebastes marinus*, × 97 ; C, a young *Blennius sp.*, × 97.

The optic nerves cross one another at a point some distance above the trabecula communis, and generally in the region where the septum merges into the base of the brain cavity. In *Salmo* the nerves are said to perforate the septum (Gaupp, 1906).

It appears certain that the origin of the interorbital septum was due primarily to the same cause which led to the development of a trabecula communis, namely the great enlargement of the eyes and the consequent lateral compression of the cranial cavity between them. The position of the eyes seems to be another important factor, since, if they were situated close to the brain cavity, the first effect of their enlargement would be an upward pressure of the cavity and a forcing together of the inner walls of the orbits. GAUPP'S[*] view that the material of the interorbital septum has been derived from the original inner walls of the orbits of the platybasic type of cranium seems to be a probable one.[†]

D. *Absorption of parts of the trabecula communis, supraorbital bars, etc., during the ontogeny.*—The absorption of more or less extensive tracts of cartilage in the orbito-temporal region during the later stages of development appears to be a much commoner phenomenon among teleostean fishes than was hitherto supposed. Generally only the hinder parts of the trabecular cartilages disappear, but portions of the supraorbital bars or even of the mesethmoid cartilage may also be involved.

The parts of the trabecular cartilages in front of and bordering on the basicranial fenestra are absorbed during the later stages of development in the following widely separated genera:—*Clupea, Amiurus, Anguilla, Exocœtus* (LAZDIN, 1913), *Siphonostoma, Gadus, Callionymus, Gobius, Cyclopterus, Gasterosteus, Pleuronectes* and *Solea.* In most of the above-mentioned genera the supraorbital bars remain intact, but these cartilages are also partly absorbed in *Gadus, Gasterosteus, Sebastes* (?), *Pleuronectes* and *Solea.*[‡] The disappearance of large tracts of cartilages in the ethmoid region, such as occurs during the metamorphosis of the larval *Anguilla*, has not been described in any other fish.

After the absorption of the hinder ends of the trabecular cartilages, the anterior part of the trabecula communis generally remains as a pointed process projecting from the posterior border of the ethmoid plate. LAZDIN (1913) concludes that this process in the larval *Exocœtus* is a new formation, and bears no relation to the original trabeculæ, which are said to show signs of degeneration at an earlier stage (*cf.* UHLMANN, 1921, p. 284); WELLS (1923) seems to have been led to the same conclusion with regard to this process in *Clupea.* A study of the conditions in *Clupea, Anguilla, Gasterosteus* and *Sebastes*, has convinced me that this view is incorrect, and that the posteriorly directed process from the ethmoid plate represents the remains of either the anterior portion of the præ-existing trabecula communis, or of a plate formed by growth of cartilage between the anterior ends of the original trabeculæ.

No complete explanation of this phenomenon of absorption has been put forward, although it has been suggested that the pressure exerted by the rectus eye-muscles

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[*] 'Anat. Hefte,' XIV, 1900, p. 553.

[†] FUCHS ('Anat. Anz.,' XLI, 1912, p. 104), who has investigated the chondrocranium of Chelonians, concludes that the interorbital septum is an entirely new formation.

[‡] In the Flatfishes the supraorbital bar of the blind side is reabsorbed almost as soon as it is developed in order to allow for the migration of the eye; later the other bar also disappears (BERRILL, 1925).

may cause the suppression of the trabecular cartilages in that region. It must be pointed out, however, that when the breaking down of the cartilages occurs the membrane bones forming the floor and roof of this region of the cranium are already developed. In this way the cartilaginous trabeculæ and supraorbital bands are replaced functionally by the parasphenoid and frontal bones respectively.

III. *The Auditory and Occipital Regions.*

A. *Postorbital and prootic cartilages ; relations of the trigeminal and facial nerves to the cartilages ; the trigemino-facialis chamber, etc.*—The name " postorbital cartilage "* has been applied in the earlier part of this paper to that part of the lateral chondrocranial wall lying between the anterior edge of the auditory capsule and the hinder margin of the optic fenestra. This cartilage appears to be developed to a greater or lesser extent in all bony fishes, and to be formed in the same way as in *Anguilla,* namely, by growth of cartilage anteriorly from the auditory capsule and downwards from the posterior part of the supraorbital bar. In *Acipenser, Polypterus, Amia, Lepidosteus, Clupea, Salmo, Galaxias* and *Anguilla* this postorbital wall is comparatively extensive, but in many of the more specialized Teleosts it is either very short or scarcely apparent, the optic fenestra and auditory capsule being closely approximated.

In many teleostean fishes *prootic cartilages*† are developed, and have the form of bars or plates of cartilage which separate the exits of the main trunks of the trigeminal and facial nerves, thus forming the anterior boundaries of the facial foramina (*q.v.*). Each of these cartilages generally extends from the anterior parachordals outwards to the lower edge of the postorbital wall, but when this wall is rudimentary or absent the prootic cartilage is connected laterally with the lower edge of the anterior part of the auditory capsule. The manner in which they are developed has been studied in only one or two forms, but it seems probable that they arise as projections from the lower edges of the thickened anterior ends of the auditory capsules, and grow inwards between the roots of the fifth and seventh nerves and finally fuse with the anterior parachordals.

In *Amia,* the prootic cartilage is developed in specimens of 9 to 10 mm. as a process projecting anteromedially from the lower edge of the front part of the auditory capsule ; this process is connected by a strand of procartilage with another projection from the triangular polar plate (PEHRSON, 1922). The subsequent chondrification of this strand completes the anterior boundary of the facial foramen. The prootic cartilages of *Amia* are certainly homologous with those of Teleosts, and their connection with the polar plates suggests that the polar cartilages belong to the parachordal rather than to

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* " Alisphenoid cartilage " *auct.*

† Prootic cartilages are present in the following Teleosts :—*Clupea, Galaxias, Salmo* (" präfaciale basicapsular Commissur," GAUPP, 1906), *Anguilla, Callionymus, Gobius, Blennius, Zoarces, Syngnathus, Siphonostoma, Gasterosteus* and *Sebastes :* they appear to be absent in *Amiurus, Gadus* and *Cyclopterus.*

the trabecular region of the cranial floor. In *Lepidosteus* the prootic cartilages are well developed, but their formation has not been described.

In the majority of teleostean fishes, and in all those forms possessing a tropibasic chondrocranium, none of the branches of the trigeminal nerve emerge through definitive foramina in the cartilage. Where a prootic cartilage is present, the maxillo-mandibulary ramus passes downwards across the anterior face of this cartilage, which is frequently provided with a well-marked indentation. Such a *prootic incisure* is present in *Galaxias*, *Salmo*, *Anguilla*, and other genera. The ophthalmic branch of the same nerve nearly always passes outwards through the hinder part of the optic fenestra.*

In all the Teleosts examined by me, with the sole exception of *Gasterosteus*, the relations of the hyoideomandibular and palatine rami of the facial nerve are similar to those already described in *Anguilla*, at least during the developmental stages. The hyoideomandibular ramus and the jugular vein at first emerge through a single *facial foramen* on each side, which is bordered anteriorly by the prootic cartilage (if developed) and posteriorly by the anterior basicapsular commissure. In comparatively late larvæ of certain Teleosts two foramina are present in this region; the anterior gives exit to the hyoideomandibular ramus, the posterior to the jugular vein and the external mandibular ramus of the lateralis element of the facial nerve. These closely approximated foramina are figured by GAUPP (1906) in a 25-mm. *Salmo*, and by LAZDIN (1913) in a larval *Exocœtus*, but it is not clear whether they arise by the division of an original single foramen as in *Anguilla*.

The small palatine ramus of the facial nerve is difficult to trace in many larval fishes, but I have found this nerve emerging through an independent, more medially situated *palatine foramen* in *Clupea*, *Galaxias*, *Salmo*, *Anguilla*, and *Gadus*.

In *Gasterosteus* (SWINNERTON, 1902) no palatine foramen is present at any stage, and the palatine and hyoideomandibular rami both pass outwards through the facial foramen, which does not become divided. This condition, which appears to be unique among Teleosts, is due to a change in the relative positions of the nerve rami and the jugular vein, and is clearly secondary (*cf.* ALLIS, 1919, p. 251).

The ophthalmic ramus of the facial nerve nearly always emerges through a small foramen in the postorbital wall as in *Anguilla*.†

The conditions in *Amia* and *Lepidosteus* are somewhat different to those described above. In *Amia* the hyoideomandibular and palatine rami at first emerge through a common foramen, which is later divided into two parts to form an anterior palatine foramen and a posterior facial foramen; at a still later stage the latter is again divided

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* In *Amiurus* (and other Siluroidea ?) the ophthalmic ramus, instead of passing outwards through the optic fenestra, runs anteriorly within the cranial cavity, and then, turning outwards, perforates the dorsolateral wall of the chondrocranium (alisphenoid cartilage, KINDRED, 1919) at about the middle of the orbit.

† The relations of this ramus in *Amiurus* are different, however; the nerve pierces the lateral chondrocranial wall (alisphenoid cartilage) near the middle of the orbit, the foramen lying close to that of the corresponding ramus of the fifth nerve.

into two portions, which give exit to the jugular vein and hyoideomandibular ramus respectively (PEHRSON, 1922, pp. 12, 18). In a 14-mm. *Lepidosteus* independent foramina for these two branches of the facial nerve are present, but, although closely approximated, these do not arise by division of a single foramen as in *Amia*.

The medial position of the geniculate ganglion in the larval *Anguilla* appears to be an unusual one; in other Teleosts, as well as in *Amia* and *Lepidosteus*, this ganglion is intimately connected with the gasserion, and lies in a more lateral (dorsal) position between the brain and the postorbital and prootic cartilages.

In the early *Leptocephalus* larvæ the ganglia connected with the trigeminal and facial nerves lie in a distinct lateral recess or *trigemino-facialis chamber*, separated from the brain cavity by a membranous wall. At a later stage this chamber becomes almost entirely obliterated. I do not find such a recess in any other larval or embryo Teleost, the ganglia being merely sandwiched between the brain and the surrounding cartilage.*

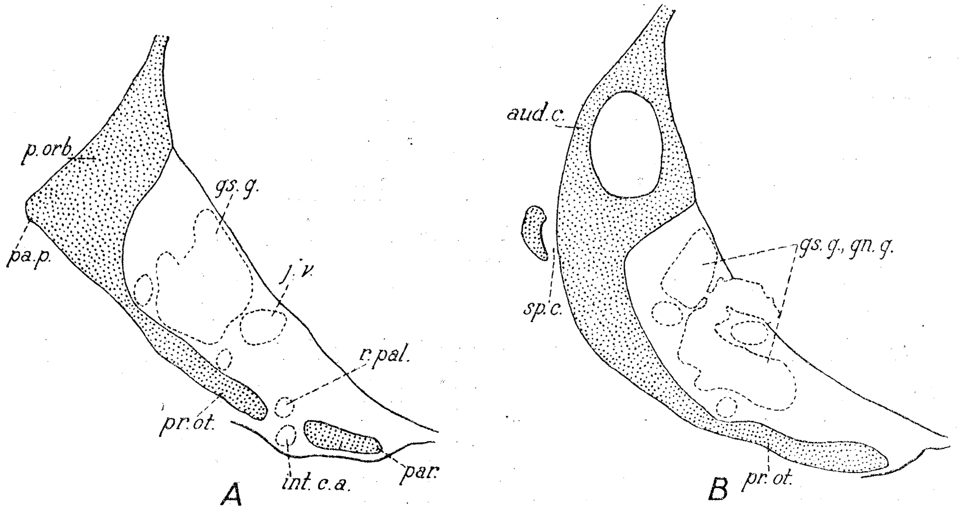

FIG. 48.—Transverse sections through the anterior and posterior regions of the trigemino-facialis chamber in the chondrocranium of a 19-mm. larva of *Amia calva*, × 45.

In *Amia*, however, a well developed chamber is present at an early stage in the ontogeny, and persists in the adult. In a 19-mm. specimen it lies below the level of the auditory capsule, the floor of which extends inwards and roofs over the posterior part of the recess (fig. 48, A, B). The conditions in *Lepidosteus* appear to be very similar, but the chamber is much deeper.

I have examined the relations of the ganglionic complex to the cranium in several young and adult Selachians, and find that this is always situated in the tegumentary mass in the angle of the orbit and on the orbital base. It is probable that the trigemino-facialis chamber of *Amia* and *Lepidosteus* has been derived from a condition somewhat similar to that found in Selachians, partly by a posterior shifting of the ganglia (which has

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* ALLIS (1903, 1919) describes a well-developed chamber in *Scomber*, and states that the inner wall (dura mater) ossifies during the later stages of development. Such an ossification is by no means general among Teleosts as supposed by VEIT (1907, p. 200).

clearly taken place), and partly by an anterior extension of the cartilage forming the auditory capsule and postorbital wall. *Anguilla* alone among Teleosts appears to have retained the extra-cranial chamber during the early stages of its ontogeny.

B. *The parachordal cartilages ; their development and relations with the notochord.*—The early formation of the *parachordals* in *Clupea* and *Anguilla* has not been investigated. In the youngest larvæ of these fishes which have been examined these cartilages are already well developed, and show no traces of segmentation. In *Salmo*, however, each of the parachordals arises from two centres of chondrification, one immediately behind the trabeculæ (anterior parachordal plate), and the other behind the exit of the vagus nerve (posterior parachordal plate). The latter, which develops first, is closely applied to the notochord ; it soon extends anteriorly into the auditory region, and becomes divided into two sections, mesotic and occipital, distinguished by a difference in the thickness of the cartilage. The anterior parachordal plate, at first free from the notochord, expands medially and posteriorly, and soon becomes fused with the mesotic section of the posterior plate (Stöhr, 1882).

The parachordals of *Gasterosteus* also arise in two sections connected by procartilage, but these do not correspond to the two parts of the same cartilages in *Salmo*. The occipital section (Swinnerton, 1902) appears to correspond to that part of the posterior parachordal plate of *Salmo* which lies behind the vagus nerve ; the large mesotic section may be compared with the anterior parachordal plate of *Salmo* plus the mesotic part of the posterior plate. In *Sebastes* and *Cyclopterus* (Uhlmann, 1921), the only other Teleosts in which sufficiently early stages have been investigated, the parachordals arise as solid masses of cartilage, and apparently from a single centre of chondrification.

In *Amia* (Pehrson, 1922) the parachordals again arise from two independent centres, which roughly correspond to the mesotic and occipital sections described in *Gasterosteus*. The occipital sections arise at a comparatively late stage, however, and are situated at some distance behind the mesotic sections, with which they are connected by mesenchyme. They subsequently fuse with the mesotic sections to complete the cranial floor. In *Lepidosteus*, the front portions of the parachordals develop as in *Amia*. Veit (1911) does not state whether the occipital parts chondrify independently, although this is probably the case. The development of the parachordals in *Acipenser* (Sewertzoff, 1895) follows the same lines as that of *Amia*.

The comparatively late development of the hinder parts of the mesotic sections in the above-mentioned Ganoids, and the still later origin of the independent occipital sections, is in marked contrast to the conditions found in the teleostean fishes. Another difference between the two groups is to be found in the relation of the cartilages to the notochord. In Teleosts the parachordals abut against the notochord for the greater part of their length at an early stage, and later fuse in front of its tip to form a solid anterior parachordal plate. In *Amia* and *Lepidosteus* (and *Acipenser* ?) these cartilages approach the notochord at a comparatively late stage, and their anterior parts remain widely separated for a lengthy period.

In *Acipenser* and *Lepidosteus* the occipital section of each parachordal at first exhibits distinct traces of segmentation, but this is never apparent in *Amia* or in Teleosts.*

The apparent backward movement of the tip of the notochord during the ontogeny is not generally due to any decrease in the length of the notochord itself; probably a certain amount of degeneration does occur at the anterior end during comparatively early stages, but in most fishes the retrogression of the rod is due either to a cessation of the growth of the notochord, or to a slowing down of the rate of growth as compared with that of the surrounding cartilages.†

In most Teleosts the parachordals fuse in front of the notochord to form a solid anterior plate as in *Anguilla*, and during the later stages cartilage is also developed to some extent above and below the notochord. The extent to which such cartilage is developed is of little importance, and varies considerably, not only in different fishes, but among individuals of the same species and of the same size (*e.g.*, *Clupea*, *Anguilla*). In *Clupea* the surrounding of the notochord appears to be accomplished by an actual fusion of the parachordals above or below it, but in *Anguilla* new cartilage is developed between the perichondria of the inner edges of the parachordals.‡ In *Amia* and *Lepidosteus*, the development of cartilage round the notochord takes place at a relatively much later stage than in Teleosts.

C. *The auditory capsules: their development, structure, and connections with the parachordal cartilages.*—In *Salmo* (Stöhr, 1882, pp. 84–86), the first rudiment of each capsule takes the form of an independent plate of cartilage situated immediately below the membranous labyrinth; this plate very soon becomes connected anteriorly with the parachordal. In the earliest stages of *Clupea* and *Anguilla* which I have studied the anterior connection between capsule and parachordal is already established, but the presence of an indistinct suture between the two cartilages suggests that the capsular cartilage is at first independent as in *Salmo*. In *Gasterosteus*, the only other Teleost in which the early development has been studied, the two sets of cartilage arise in continuity, the capsular rudiment never being independent (Swinnerton, 1902, p. 511).

Among the Ganoids, the cartilaginous rudiment of the capsule in *Amia* is for a short time independent of the parachordal (Pehrson, 1922), but in *Lepidosteus* (Veit, 1911) and *Acipenser* (Gaupp, 1906, p. 651) the two arise in continuity. Of the Selachians,

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* Sewertzoff (1899) speaks of the *segmented* occipital regions of the parachordals of the Selachian fishes *Squalus* and *Pristiurus*, but the work of Hoffmann (1896) and Wijhe (1922) has not confirmed this.

† I have carefully measured the notochord at different stages in *Clupea* and *Anguilla*, and find that during the larval development this undergoes an actual increase in length; Swinnerton (1902) found the same in *Gasterosteus*. Pehrson (1922, p. 32) has measured the notochord in *Amia*, and finds that it undergoes a relative retrogression throughout the development of the cranium as in Teleosts, but that absolute reduction in length occurs during the later stages. No decrease in the length of the notochord has been observed in *Lepidosteus*; in *Polypterus* considerable retrogression is said to take place (Pehrson, 1922, p. 16).

‡ Some authors speak of an actual chondrification of the notochordal sheath, but I have not observed this process in any Teleost.

the early development of the auditory capsule has been described only in *Squalus* and *Scyliorhinus*. In *Squalus* (WIJHE, 1922, p. 294) the base of the capsule (lamina basiotica) arises as an outgrowth from the parachordal, but independent nuclei are also developed at the anterior and posterior ends of the auditory organ; in *Scyliorhinus* (GOODRICH, 1918, p. 24) the base arises in the same manner, but the independent chondrifications are not developed.

Whether the auditory capsule arises independently or in conjunction with the parachordal, the first connection between the two cartilages in Teleosts as well as in *Amia* and *Lepidosteus* takes the form of a cartilaginous bar situated immediately behind the exit of the facial nerve—the *anterior basicapsular commissure.* As in *Anguilla,* the *posterior basicapsular commissure,* lying behind the exit of the glossopharyngeal nerve, arises at a considerably later stage. The development of this posterior commissure, which nearly always replaces a præ-existing connection of connective tissue or procartilage, completes the boundary of a fenestra in the floor of the auditory capsule—*basicapsular fenestra.*[*] The posterior commissure generally separates the exits of the glossopharyngeal and vagus nerves, so that the former at first emerges through the hinder end of the basicapsular fenestra; when this is subsequently closed by growth of cartilage, a small foramen remains for the passage of the glossopharyngeal nerve.[†]

The comparatively late development of the posterior basicapsular commissure, which is a constant feature in the ontogeny of bony fishes, appears to be connected with the change in position undergone by the glossopharyngeal ganglion during the development. By moving slowly in a posterior direction over the region which would normally be occupied by the commissure, the presence of the ganglion prevents for a time the development of the cartilaginous connection (*cf.* VEIT, 1911, p. 98). The persistence of the basicapsular fenestra for some time after the posterior commissure has been completed is due (in Teleosts at least) to the marked growth of the sacculus at this stage. In *Clupea, Salmo,* and *Anguilla* the sacculus projects downwards well into the fenestra, and the cartilage which later surrounds it and closes the fenestra is considerably thinner than that forming the remainder of the capsular floor.

Some authors have laid great stress on the extent to which an internal pit or saccular fossa and an external saccular bulla are developed. I find these structures strongly or moderately marked in *Lepidosteus, Clupea, Gobius, Cyclopterus* and *Sebastes,* but scarcely

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[*] PARKER (1873, p. 118) first referred to this fenestra in *Salmo* as a "primordial fenestra ovalis"; STÖHR (1882, p. 87) concludes that it corresponds to the "fenestra vestibuli" of higher vertebrates, or at least to its first formation.

[†] In *Lepidosteus* a complete fenestra is never present in the capsular floor, the base of the capsule having become joined to the parachordal along its entire length at the time when the posterior commissure is developed. The region below the sacculus, however (*i.e.,* that normally occupied by the fenestra), remains procartilaginous when the commissure is fully chondrified (VEIT, 1911).

The stage at which a fenestra is present is also very transitory in the specialized Syngnathidæ among the Teleosts, but a minute foramen, which is clearly homologous with the larger fenestra, is apparent until a fairly late stage.

apparent in *Amia, Anguilla* and *Callionymus*. The extent to which these and other projections or fossæ are present on or in the capsular wall seems to be of no importance, the cartilage forming the capsule being merely closely moulded to the shape of the underlying membranous labyrinth. In many Teleosts the course of the semi-circular canals can be clearly traced externally.

In a 3·6-mm. *Gasterosteus* (SWINNERTON, 1902, p. 510) an oblique ridge of cartilage divides the mesotic section of the parachordal into two parts, the more postero-lateral of which supports a part of the auditory labyrinth. In a slightly older stage (*t.c.*, p. 512), this part of the parachordal has spread outwards below the labyrinth, and, according to this author, is to be regarded as a part of the auditory capsule.

In the early stages of *Anguilla* I find that the outer edge of the parachordal assists in the support of the auditory organ, and that when the basicapsular fenestra is finally closed this is effected partly by growth of cartilage outwards from the parachordal. Again, in early larvæ of *Clupea* a part of the labyrinth rests on the parachordal cartilage. I do not regard this cartilaginous support as a part of the capsule itself, but rather as a part of the parachordal which has secondarily taken on the function of supporting the inner edge of the labyrinth. It may be mentioned, however, that in Selachians a part of the floor of the capsule is said to be formed as an outgrowth from the parachordal cartilage.

An interesting modification of the anterior region of the capsular floor is found in *Clupea*, and is connected with the development of the anterior extensions of the air-bladder. In a 20-mm. larva examined by me the so-called prootic vesicle is partially embedded in a mass of cartilage formed by the anterior basicapsular commissure and the front part of the capsular base. The narrow duct connecting this vesicle with the main air-bladder passes obliquely through the floor of the capsule in a postero-ventral direction. The vesicle itself is not completely surrounded by cartilage at any stage, its final encasement being effected when the prootic bone develops.*

In *Acipenser*, *Amia* and *Lepidosteus* the whole of the membranous labyrinth is finally roofed over by cartilage, but in many teleostean fishes this roof is incomplete anteriorly. The posterior parts of the auditory capsules nearly always fuse medially above the brain to form a more or less extensive synotic tectum (*q.v.*).

In *Amia* and *Lepidosteus* there is a well-marked groove on the external face of the auditory capsule for the reception of the articular head of the hyomandibular. This groove is roofed over by a longitudinal ridge of cartilage, which is continuous posteriorly with the prominence marking the position of the lateral semicircular canal, and ends anteriorly in a short knob-like process projecting outwards from the postorbital wall.†

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* The relations between the air bladder and the labyrinth, etc., in the larval *Clupea* have been described in detail by BEAUFORT ('Morph. Jahrb.,' XXXIX, 1909, pp. 620–628, figs.), and MAIER AND SCHEURING ('Wiss. Meeresunt. Kiel,' N.F., XV, 1923, Abt. Helgoland, No. 6, 22 pp. 2 pls., 12 text-figs.); the conditions in the adult fishes have been studied by RIDEWOOD ('J. Anat. Physiol.,' XXVI, 1892, pp. 26–42, text-figs.); and TRACY ('J. Morph.,' XXXIII, 1920, pp. 439–474, pls. I–V).

† "Processus postorbitalis," VEIT, 1911.

This *parotic ridge* is pierced just in front of the hyomandibular by a canal in which the "recessus dorsalis spiracularis" is situated.* In teleostean fishes the articular surface is generally quite flat, although in *Salmo* the anterior head of the hyomandibular fits into a hollow in the capsular wall. The parotic ridge and process may be developed (*e.g.*, *Clupea, Galaxias, Salmo, Ictalurus,*† *Anguilla*, etc.), but are never prominent. When present, the parotic process serves as a basis for the support of certain muscles connected with the hyomandibular.‡

The cavity of the auditory capsule always communicates directly with the cranial cavity in Teleosts, and a medial cartilaginous wall, if developed at all, is confined to the extreme anterior and posterior corners. In *Amia, Lepidosteus* and *Polypterus* short medial partitions are again developed anteriorly and posteriorly, but their extent is somewhat greater. The capsular and cranial cavities of Selachians communicate by a wide fenestra during the embryonic stages, but a complete medial wall of cartilage is later developed, and only a small foramen remains for the passage of the auditory nerve (SEWERTZOFF, 1897, 1899).

Contrary to the opinion expressed by KINDRED (1919, p. 16) and others, I conclude that the conditions found in *Amia, Lepidosteus* and Teleosts have been derived phylogenetically from a condition in which a more or less complete wall separated the cranial cavity from that of the capsule. The reduction of this wall appears to have been brought about by the inward expansion of the membranous labyrinth, and the fact that in bony fishes this expansion takes place at a comparatively early stage would account for the non-appearance of a medial cartilaginous wall at any period of the ontogeny.§ The general narrowing of the cranium in bony fishes may have been a second factor with which the reduction of the inner wall is correlated.

The cartilaginous *semicircular septa*, varying from one to three in number, are present in all bony fishes.‖ The lateral septum always occupies a vertical position, but the anterior and posterior septa may be either horizontal or oblique.

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* Both the parotic process and parotic ridge are well developed in young and adult *Polypterus* (BUDGETT, 1902—"pterotic ridge"; LEHN, 1918).

† The development of a parotic ridge above the hyomandibular is apparently of little importance: it is well developed in the larval *Amiurus* (KINDRED, 1919, p. 16), but is entirely wanting in the larval *Ictalurus*, a closely related genus (RYDER, 1887, p. 541).

‡ For further notes on the parotic ridge in various fishes see ALLIS (1920—"Spheno-pterotic ridge").

§ The inward expansion of the labyrinth would also explain the fact that a portion of the auditory organ is supported by the parachordal in some fishes.

‖ Three septa are all fully chondrified in *Acipenser, Polypterus, Amia, Lepidosteus, Clupea, Galaxias Salmo, Gymnarchus, Amiurus, Sebastes, Pleuronectes* and *Solea*; in *Anguilla, Syngnathus, Siphonostoma, Gadus, Cyclopterus* and *Gasterosteus* the anterior septum is absent at all stages of development. In a young *Gobius*, and in a *Callionymus* of 10 mm., I find only the lateral semicircular septum chondrified, the anterior being absent and the posterior composed of fibrous connective tissue.

D. *Occipital processes and lateral cartilages of the occipital region ; relations of the glossopharyngeal and vagus nerves to the chondrocranium.**—In those Teleosts in which early stages have been studied the lateral parts of the occipital region arise as a pair of dorsally directed processes from the parachordals—the *occipital processes*,† which later fuse with the posterior parts of the auditory capsules as in *Anguilla*. In *Clupea*, *Salmo* and *Anguilla* these processes also fuse medially and take part in the formation of the hinder portion of the synotic tectum. In some more specialized forms (*e.g.*, the Syngnathidæ), in which this tectum is either reduced or wanting, the fused occipital processes form an independent occipital arch.‡

In *Amia* and *Lepidosteus* similar occipital processes are developed, but these arise at a much later stage than the same elements in Teleosts. They become fused with the posterior ends of the auditory capsules in the same manner. In *Amia* (PEHRSON, 1922) the two processes become joined medially to form an occipital arch, which remains separated from the synotic tectum for some time by a large foramen. In *Lepidosteus* (VEIT, 1911) no separate arch is formed at any stage, the conjoined occipital processes merging directly into the hinder cranial roof.

The foramen for the ninth nerve in *Anguilla* has been shown to represent a remnant of the large basicapsular fenestra, and the jugular foramen for the tenth nerve has been described as being formed by the fusion of the occipital process with the auditory capsule above the vagus and with the parachordal below it. Comparing these processes with those occurring in related fishes, we find that in *Salmo* the two foramina are formed exactly as in *Anguilla*, but in *Clupea* the conditions are somewhat different.

In a 30-mm. larval *Clupea* the auditory capsules extend for some distance posteriorly beyond the exits of the vagus nerves. Both the ninth and tenth nerves on each side pass outwards through a groove§ in the anterior edge of the occipital process, which in this region separates the brain cavity from the hinder part of the auditory capsule (fig. 49, A, *n.* IX, X). The nerves then run posteriorly in a short canal situated in the cavity of the capsule (fig. 49, B), and finally emerge through a foramen situated ventrally between the parachordal and the extreme posterior end of the auditory capsule (fig. 49, C).

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* The important question of the metamerism of the occipital region of the fish chondrocranium is not dealt with in this paper, but the following papers, which have been reviewed by GAUPP (1906), may be mentioned :—WIJHE (1882), STÖHR (1882), SAGEMEHL (1884, 1885, 1891), GEGENBAUR* (1887), SEWERTZOFF* (1895), FÜRBRINGER* (1897), WILLCOX (1899), DOHRN* (1901), FRORIEP (1901), and SCHREINER (1902). For references to the various papers by authors marked with an asterisk, see GAUPP (1906). In more recent years the problem has been studied by NUSBAUM (1908), VEIT (1911), KINDRED (1919), and UHLMANN (1921), among others.

† " Occipitalbögen," STÖHR, 1882 ; " pila occipitalia," UHLMANN, 1921.

‡ Although a well-developed synotic tectum is present in *Gasterosteus*, the occipital processes are said to take very little part in its formation (SWINNERTON, 1902, p. 515).

§ WELLS (1923, p. 1219, fig. 3, F X) describes and figures a complete jugular foramen in the occipital process of a 10-mm. larva, but a study of his preparations shows that this is erroneous, the nerves emerging through a groove in the anterior face of the cartilage.

Among other Teleosts, *Gymnarchus, Amiurus,** *Gadus* and *Cyclopterus* exhibit the same conditions as *Salmo* and *Anguilla,* and the independent foramina for the ninth and tenth nerves appear to be formed in a similar manner. In *Gasterosteus,* however, the fusion of the posterior end of the auditory capsule with the parachordal on the one hand, and with a lateral projection from the occipital process on the other, completes a common foramen for the exit of both nerves. This foramen is never divided by growth of cartilage, the two nerve exits being finally separated only when the exoccipital bone is developed (SWINNERTON, 1902).†

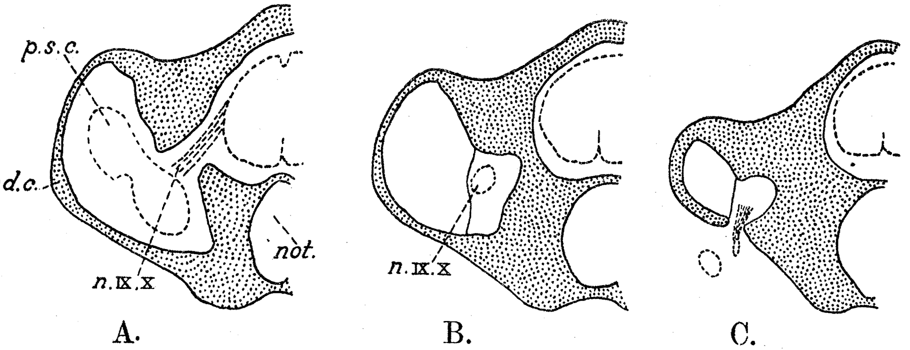

FIG. 49.—Transverse sections through the region of the glossopharyngeal and vagus nerve exits on the left side of the chondrocranium of a 30-mm. larva of *Clupea harengus,* × 40.

I regard the conditions in *Salmo* and *Anguilla* as the more primitive, and conclude that the common foramen for both nerves in *Clupea* and certain other Teleosts is a secondary formation. This conclusion is supported by a study of these foramina in *Amia* and *Lepidosteus,* in which they are quite separate and arise in exactly the same way as in *Anguilla.*

IV. *The Roof of the Chondrocranium.*

Before discussing the origin and homologies of the cartilaginous cranial roof in bony fishes, it will be convenient to review briefly the development, form and extent of this roof in the different groups. These groups may be dealt with in the following order :—*Euselachii* (recent Selachians); Cladistia (*Polypterus*); Palæopterygii (*Acipenser, Polyodon*); and Neopterygii (*Amia, Lepidosteus,* and Teleosts).

Apart from small foramina connected with nerves, blood-vessels, endolymphatic ducts, etc., the roof of the cranium in adult Selachians‡ is complete except at the extreme

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* In the closely related genus *Ictalurus,* a common foramen apparently serves for the exit of both ninth and tenth nerves (RYDER, 1887, pl. XXX).

† In *Syngnathus* (KINDRED, 1921) and *Siphonostoma,* both nerves emerge through a common foramen, but the manner in which this is formed is not known.

‡ I have referred to the following papers dealing with the skull of adult Euselachii :—GEGENBAUR (1872); HOFFMAN (1912—*Pristis, Pristiophorus*); DANIEL ('J. Morph.,' XXVI, 1915, pp. 447-476, 8 pls.—*Heterodontus*); DANIEL ('Berkeley Univ. California Pub. Zool.,' XVI, 1916, pp. 349-370, pls. XXVII-XXIX—*Heptanchus*); and WELLS ('J. Morph.,' XXVIII, 1917, pp. 417-436, 3 pls.—*Squalus*). I have also examined skulls of the following genera :—*Notidanus, Heterodontus, Centrophorus, Mustelus, Chiloscyllium, Ginglymostoma, Pristiurus, Squatina, Raia* and *Torpedo.*

anterior end, where there is a fairly extensive area which is closed merely by membrane (anterior or præfrontal fontanelle).* The exact manner in which the roof is developed has not been clearly described; the hinder portion appears to arise by the medial fusion of the auditory capsules, the anterior part being developed from the sphenolaterals.

PARKER (1876, p. 219, pl. XL, fig. 4) describes and figures a large fontanelle in the roof of the orbitotemporal region of an embryo *Raia*, which is said to be separated from the præfrontal fontanelle by a transverse "cartilaginous beam." The same author figures both fontanelles in the adult skull (*t.c.* pl. XLI, fig. 3), but in the specimen examined by me the more posterior of the two is closed by thin cartilage.

In *Callorhynchus* (SCHAUINSLAND, 1903) even the præfrontal fontanelle becomes closed by cartilage, the cranial roof being entire in the adult.

In *Acipenser*, the maximum development of cartilage in the roof is found in the adult stage, as in the Selachians, and a complete cartilaginous tectum is present in addition to the overlying bony roof. The development of this roof has not been clearly described. In the adult *Polyodon* (BRIDGE, 1879, pl. LVI, fig. 5),† on the other hand, the cartilaginous roof is provided with three fontanelles; an anterior, median one, which is probably homologous with the præfrontal fontanelle of the Selachian skull, and paired "parietal foramina," which may represent the remains of an earlier existing posterior fontanelle.

In *Polypterus*, the maximum development of cartilage in the cranial roof seems to be represented in the 76-mm. specimen figured by LEHN (1918, fig. 1). The synotic tectum is separated from the ethmoidal roof by a large fontanelle which is divided into two sections by a typical epiphysial bar. In a 90-mm. example this bar is no longer connected on either side with the supraorbital bars, and forms an independent piece of cartilage lying in the centre of a single large fontanelle.‡ In the adult condition the cartilaginous roof is still further reduced in the orbitotemporal region (ALLIS,§ 1922, pl. VII, fig. 10).

Turning to the lower Neopterygian fishes, we find that in *Amia* and *Lepidosteus* the cartilaginous roof is practically complete in the adult. In *Amia*, the first trace of the roof takes the form of a narrow transverse bar of cartilage above the paraphysis (*paraphysial bar*), formed by the inward growth and fusion of the ectethmoids, and a second above the posterior part of the epiphysis (*epiphysial bar*), the development of which has been previously described. Cartilage is soon developed in the region between

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* Since this membrane is generally more or less intimately connected with the epiphysis, the fontanelle would seem to lie actually in the cranial roof, and not in the anterior wall of the cranial cavity as suggested by ALLIS ('Anat. Anz.,' XLIV, 1913, pp. 322-328).

† BRIDGE, T. W., "On the Osteology of *Polyodon folium*," 'Phil. Trans. Royal Soc.,' vol. 169, pt. 2, 1879, pp. 683–733, pls. LV-LVII.

‡ POLLARD (1892, p. 400, figs. 11, 30) figures a specimen with the roof in this condition. He regards the independent plate of cartilage as indicating "the former existence of a complete cartilaginous tegmen cranii."

§ ALLIS, E. P., "The Cranial Anatomy of *Polypterus* . . . ," Journ. Anat.,' LVI, 1922, pp. 189-294, pls. III–XXIV.

these bars, resulting in a massive anterior roof, in which a small foramen persists immediately above the epiphysis. This roof is separated from the more posterior synotic tectum by a large fontanelle (fig. 50, A), which is later divided by a median longitudinal bar of cartilage. Finally, the paired fontanelles thus formed are closed by growth of cartilage inwards from the lateral parts of the chondrocranium, and the epiphysial foramen also disappears (PEHRSON, 1922). The development of the cranial roof in *Lepidosteus* takes place in a somewhat similar manner (VEIT, 1911), differing chiefly in the formation of its more anterior parts (fig. 50, B).

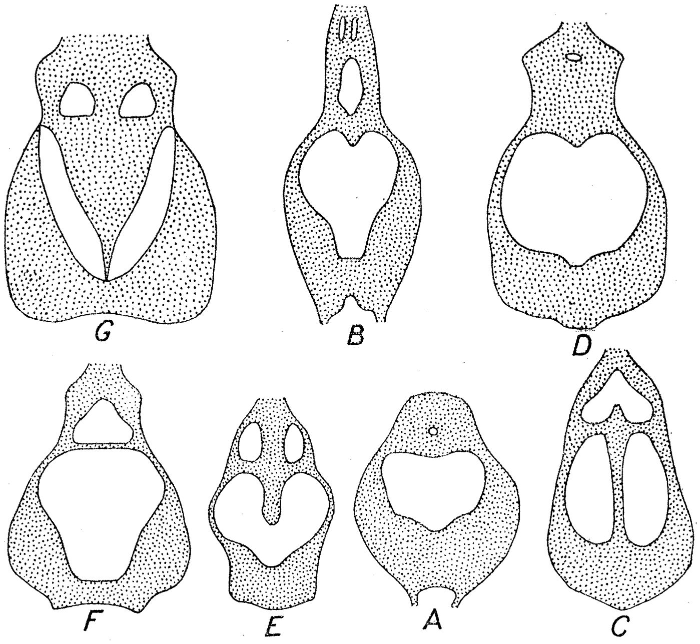

FIG. 50. Diagrammatic representations of the cartilaginous chondrocranial roof in A, a 25-mm. *Amia calva*, × 25 (after PEHRSON); B, a 20·5-mm. *Lepidosteus osseus*, × 33 (after VEIT); C, a 30-mm. *Clupea harengus*, × about 35; D, a 25-mm. *Salmo*, × 40 (after GAUPP); E, a 49th day *Gymnarchus niloticus*, × 20 (after ASSHETON); F, a 32-mm. *Amiurus nebulosus*, × — (after KINDRED); G, a 56-mm. *Cyclopterus lumpus*, × about 25 (after UHLMANN).

In the Teleosts, we find all degrees of development of cartilage in the cranial roof, ranging from the massive roof of *Cyclopterus* (fig. 50, G), in which the maximum development of cartilage is said to occur in the adult (UHLMANN, 1921), to the condition found in *Syngnathus* and *Siphonostoma*, in which practically no roofing cartilage is apparent in the orbitotemporal region, and even the synotic tectum is considerably reduced. The form and extent of the chondrocranial roof in certain teleostean fishes is illustrated in the accompanying figures (fig. 50). In these fishes the cartilaginous roof is rarely completed as in *Amia* and *Lepidosteus*, the fontanelles persisting until the membrane roofing bones are developed. In many cases a considerable reduction of the cartilaginous roof takes place during the ontogeny.

Omitting the most anterior portion of the roof in the larval *Lepidosteus*, which is formed by the medial growth and fusion of the lateral walls of the ethmoid region, and which lies wholly anterior to the paraphysis, six distinct sections may be recognised as contributing to the formation of the cranial roof in Neopterygian fishes. These sections are: (1) a paraphysial bar; (2) an epiphysial bar; (3) a median, longitudinal bar connecting the paraphysial and epiphysial bars; (4) a median, longitudinal bar joining the epiphysial bar to the synotic tectum (sometimes incomplete); (5) a synotic tectum, formed from the auditory capsules; (6) an occipital tectum, derived from the occipital processes, and soon becoming fused with the synotic tectum.

A paraphysial bar, which is strongly developed in *Amia* and *Lepidosteus*, is generally absent in teleostean fishes, the posterior extension of the mesethmoid cartilage preventing the medial fusion of the ectethmoids.*

The epiphysial bar was considered by SAGEMEHL (1885, 1891) to be an element found only in the crania of the fishes of the order Ostariophysi, but, if we consider the developmental stages, this cartilage has been found in a number of widely separated teleostean genera, as well as in *Amia*, *Lepidosteus*, and *Polypterus*.† It is generally connected laterally with the supraorbital bars, but may be quite independent (*e.g.*, *Gadus*, *Siphonostoma*). In *Acipenser* the epiphysial bar seems to be indicated in a 14½ mm. specimen described by PARKER (1882*a*, p. 157). The "transverse beam" of PARKER's description of the cranium of *Raia* may be homologous with the epiphysial bar, with which it corresponds in form and position.

An anterior longitudinal bar is developed in only a few genera,‡ and appears to arise as an outgrowth from the anterior ethmoidal roof. The posterior longitudinal bar, which may be incomplete (*e.g.*, *Salmo*, *Gymnarchus*), generally grows backwards from the middle of the epiphysial bar.§

The anterior fontanelle in the cranial roof of bony fishes (or at least a part of it) seems to correspond to the præfrontal fontanelle of the Selachian skull. In the Selachians the fontanelle occupies an antero-dorsal position, and lies partly between the olfactory capsules, but in all other fishes it is completely dorsal in position, and is situated behind the ethmoid region; in all fishes, however, the fontanelle is related to the epiphysis. The change in position would have been brought about largely by the development and posterior expansion of a massive mesethmoid cartilage, which would tend to push the

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* This bar is present during the early stages of the ontogeny in *Cyclopterus* (UHLMANN, 1921).

† An epiphysial bar is developed at one stage or another in the following Teleosts, among others:—*Clupea*, *Galaxias*, *Salmo*, *Coregonus* (BAYER—'Sitzber. K. Böhm. Ges. Wiss. Prag,' 1888 (1889), pp. 401-403, 1 pl.), *Gymnarchus*, *Cyclothone* (GIERSE—'Morph. Jahrb.,' XXXII, 1904, pp. 602-688, pls. XIV-XVI), *Argyropelecus* (HANDRICK—'Zoologica,' XIII, Heft 32, 1901, 68 pp., 6 pls.), *Esox* (WALTHER, 1883), *Exocœtus*, *Gadus*, *Motella*, *Siphonostoma*, *Regalecus* (PARKER—'Trans. Zool. Soc.,' XII, 1886, pp. 5-33, pls. II-VI), *Hoplostethus* (SUPINO—'Ric. Lab. Anat. norm. Roma,' IX, fasc. 3, 1903, pp. 217-232, 1 pl.), *Atherina* (POUCHET, 1878), *Gobius*, *Zoarces*, *Gasterosteus*, *Cyclopterus*, *Sebastes*, and *Lophius*.

‡ *Cyclothone*, *Gymnarchus*, *Atherina*, *Gobius*, *Cyclopterus*, and *Lophius*, among others.

§ This bar is present during the developmental stages of *Clupea*, *Salmo*, *Atherina*, *Gobius*, *Gasterosteus*, *Cyclopterus*, and *Sebastes*; it has been described in the adult cranium in the following genera: *Coregonus*, *Osmerus*, *Alepocephalus*, *Cyclothone*, *Regalecus*, and *Hoplostethus*.

original præfrontal fontanelle upwards and backwards, until it reached the position characteristic of the bony fishes. The closing of the fontanelle by cartilage in *Amia*, *Lepidosteus*, and certain Teleosts, must be a secondary condition, and seems to be correlated with the form and position of the epiphysial organ.

On the evidence derived from a study of the development of the cartilaginous roof in a number of fishes, I conclude that the roof of the bony fish chondrocranium with its extensive fontanelles, has been derived by the reduction of a more massive cartilaginous roof, which probably possessed two small fontanelles, the more anterior of which was related to the epiphysis.*

The fact that no process of fenestration occurs during the ontogeny of the lower Neopterygian fishes, or of the more primitive Teleosts, may be readily understood if the development of the bony cranial roof is considered. It is conceivable that, between the hypothetical ancestor with the simple, box-like cranium, and the bony fishes, an intermediate stage intervened in which a complete cartilaginous roof was present in addition to a more superficial bony one.† The closer approximation of the roofing bones to the cartilaginous tectum, and their earlier appearance in the ontogeny, would tend to preserve the fontanelles normally present only during the early stages of development, and to obviate the necessity for or actually prevent the further growth of cartilage. Further, by the development of dermal bones in connection with the cranial roof, and their adequate support by the lateral orbitosphenoids, etc., the primary cartilaginous roof would be replaced functionally by the bony one and rendered superfluous. By a subsequent shortening of the ontogenetic record, to meet the exigencies of a larval life, the stage at which a more or less complete cartilaginous roof is present has been omitted from the ontogeny of many bony fishes.‡

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* SWINNERTON (1902, pp. 562–568) has reviewed this question at some length, and adopts a different conclusion. He is led to believe that the ancestor which gave rise to the existing fishes possessed, not a simple box-like cranium, but a cranium with "two dorsal fontanelles separated by a band of cartilage usually related to the epiphysis; also lateral fontanelles for the transmission of optic, trigeminal, facial, and auditory nerves; and a pituitary fontanelle." He finds such an ancestral form in some "primordial Marsipobranch," and claims that the form and development of the chondrocranium of the Lamprey supports this view. It is impossible to deal adequately in this paper with the various points raised by SWINNERTON, nor does the whole question appear to merit the importance placed upon it by that author. My own researches have led me to regard the bony fish chondrocranium as having been derived from a simple box-like cranium of the Selachian type, generally through a process of progressive fenestration.

† This condition is realized among living fishes in some of the members of the sub-class Palaeopterygii (*e.g.*, *Acipenser*), which are the most generalized of the existing Pisces.

‡ It must be noted that the longitudinal bars of cartilage which persist in the cranial roof of many Teleosts lie between the anterior and posterior pairs of dermal roofing bones, *i.e.*, between the frontals and parietals respectively.

The preservation of the epiphysial bar in many Teleosts is considered by SAGEMEHL to be connected with the need for a support for the blood vessels passing to the brain, and in this connection it is of interest to note that in *Amia* and *Clupea* each supraorbital bar is pierced by such a vessel immediately opposite its junction with the epiphysial bar. The retention of this bar, however, would seem to be also correlated with the protection of the epiphysial organ, a part of which almost invariably lies below the cartilage.

The absence of the præfrontal or anterior fontanelle in *Amia* and *Lepidosteus* is of little importance, and is probably a secondary condition. If we consider the massive chondrocranium of the adult *Cyclopterus* it is clear that the obvious postulate that mass of cartilage is a primitive character cannot be blindly accepted. In this connection it is interesting to note that whereas in *Salmo* (and to a lesser extent in *Galaxias*), the anterior fontanelle is practically closed in the adult and the cranium remains largely cartilaginous, in the adult *Clupea*, presumably a more primitive Teleost, the cartilage is almost entirely replaced by bone and the fontanelle is never closed.

Further evidence for the view that a complete cartilaginous roof was originally present, at least in the hinder part of the cranium, is to be found in the manner of development of the supraoccipital bone in certain teleostean fishes. This cartilage bone generally arises in connection with the posterior longitudinal roofing bar, or with the synotic tectum, but subsequently extends anteriorly in some forms into regions where no cartilage exists or has ever existed during the developmental stages, thus indicating a formerly greater extension of cartilage in this region (*cf.* SWINNERTON, 1902, p. 520).

V. *The Visceral Arches.*

A. *Præmandibular elements—præmaxillary and maxillary cartilages, labial cartilages, etc.*—In the anterior region of the chondrocranium of bony fishes there may be developed certain small paired or unpaired cartilages, which may perhaps correspond to the labial cartilages of Selachians, regarded by many authorities as representing the remains of præmandibular visceral arches.

These præmandibular elements are of three kinds: (1) paired *præmaxillary cartilages*, which may fuse together to form a single, median rostral cartilage; (2) one to three pairs of *submaxillary cartilages*, developed below the maxillary bones in certain Teleosts (*Gymnotus*, *Catostomus*, *Perca*—SAGEMEHL, 1885, 1891); these probably correspond collectively to the posterior upper labial cartilages of Selachians; (3) a pair of small *labial cartilages*, probably homologous with the lower labials of Selachians; these are developed in the folds at the angles of the mouth in certain Teleosts, *e.g.*, *Gasterosteus* (SWINNERTON, 1902, p. 547), *Gadus* (BROOKS,* 1883, p. 179), and other genera (*cf.* STANNIUS,† 1854).‡ In the Siluroid fishes certain of these præmandibular elements serve as skeletal supports for the barbels.

In this paper I propose to deal only with the præmaxillary cartilages.§

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* BROOKS, H. J., "The Osteology and Arthrology of the Haddock," 'Proc. R. Dublin Soc.,' N.S., IV., pp. 166–196.

† STANNIUS, H., "Handbuch der Anatomie der Wirbelthiere," Berlin, 1854.

‡ In *Anguilla, Syngnathus, Siphonostoma*, and other Teleosts, these cartilages are represented by condensed cellular masses which never become chondrified.

§ Among the different papers dealing with the labial cartilages and other præmandibular elements, the following may be mentioned:—ALLIS (1917; and 'Q. Journ. Micr. Sci.,' LXII, 1916, pp. 95–114, pl. VI); GEGENBAUR (1872); KESTEVEN ('J. Anat.' LVI, 1922, pp. 307–324, 5 figs.); POLLARD (1892; 1895a; 'Anat. Anz.,' IX, 1894, pp. 349–359; 'Verh. Anat. Ges.,' IX, 1895, pp. 232–235); and SAGEMEHL (1885, 1891).

Paired præmaxillary cartilages have been described in *Salmo* (Parker, 1873, "subrostral cartilages"; Gaupp, 1906), *Gasterosteus*, and *Cyclopterus* (Uhlmann, 1921, p. 294); I have found them also in *Anguilla* and *Galaxias*. In all these fishes the cartilages are closely related to the posterior ends of the præmaxillary bones, which are frequently embedded in the substance of the cartilage. They arise at a comparatively late stage of development, sometimes subsequent to the first appearance of the præmaxillary bones (*e.g.*, *Salmo*).

In other teleostean fishes a small, median, and generally independent piece of cartilage may be developed above the anterior part of the ethmoid region.* In those forms in which this element is present,† paired præmaxillary cartilages appear to be invariably wanting, and it seems reasonable to suppose that the unpaired cartilage has arisen through the fusion of the paired præmaxillary elements. In this connection it is interesting to note that in *Pleuronectes* and *Solea* the unpaired præmaxillary (rostral) cartilage has been shown to arise as a "paired rudiment" (Berrill, 1925, p. 226).

In all the Teleosts examined by me the median præmaxillary cartilage is again intimately connected with the developing præmaxillary bones, and particularly with their ascending processes. Further, in all the genera in which this cartilage is present, the ascending processes of the bones are well developed, and the mouth is more or less protractile; this cartilage, by assisting the free movement of the præmaxillary bones on the ethmoid region of the cranium, facilitates the protrusion and retraction of the jaws.‡

The præmaxillary cartilages of Teleosts probably correspond to the anterior upper labial cartilages of Selachians,§ and the præmaxillary bones of these fishes would appear to have arisen mainly as membrane bones, but also in part as ossifications of the labial cartilages.||

B. *The development of the mandibular and hyoid arches.*

1. *Mandibular Arch.*—Among Teleosts the early stages in the development of this arch have been studied in only four genera—*Clupea*, *Salmo*, *Gasterosteus* and *Sebastes*. An

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* Rostral cartilage, rostrale, Schnauzenteil, præmaxillary piece.

† A rostral cartilage has been recognised in *Silurus*, *Callichthys*, *Chætostomus*, and *Labrus* (Pollard); *Macrurus* (Sagemehl); *Belone* and *Malthæa* (Stannius); *Syngnathus* (Kindred); *Sebastes* (Mackintosh); *Pleuronectes* and *Solea* (Berrill): Sagemehl (1891) also records its occurrence in representatives of the families "Cyprinidæ, Scombresocidæ, Cyprinodontidæ, Scopelidæ, Acanthopteridæ," and among members of the order Plectognathi. I have found it also in *Gadus*, *Gobius*, and *Zoarces*.

‡ The single præmaxillary cartilage present in the Syngnathid fishes, where the suction method of feeding requires the free movement of the bones of the jaws, clearly acts as a roller on which the ascending processes slide.

§ Sagemehl (1891) compares the single præmaxillary cartilage of Teleosts with the small, median element lying between the anterior ends of the palatoquadrate bars in *Heptanchus*; Kindred (1921, p. 438) also supports this view.

|| Kesteven ("A new Interpretation of the Bones in the Palate and Upper Jaw of Fishes, Part I," 'J. Anat.,' LVI, 1922, pp. 307-324, 5 figs.) has suggested that the præmaxillary and maxillary bones are homologous with the anterior and posterior pairs of labial cartilages of Selachians.

examination of preparations of larval *Clupea* and *Sebastes*, on which the papers of WELLS (1923) and MACKINTOSH (1923) were based, has led me to disagree with certain of their conclusions. For this reason it will be necessary to redescribe briefly the processes of development of the arch in these fishes, and to contrast them with those of *Salmo* and *Gasterosteus*.

In a 5-mm. *Clupea* (fig. 51, A) the mandibular arch is already clearly differentiated and well chondrified, but only the quadrate section of the upper jaw is developed, and shows no trace of a palatine process. WELLS (1923, p. 1218) describes the quadrate as being continuous with Meckel's cartilage at this stage, but I can detect a distinct suture between them, although the two elements are very closely connected. The posterior end of the quadrate is completely fused with the hyomandibular. In a 10-mm. larva the mandibular arch has undergone little change, but the first trace of the palatine section of the palatoquadrate has appeared in the form of a narrow rod lying below the ectethmoid region of the neurocranium, with which it is joined by connective tissue (fig. 51, B); the posterior end of this rod is connected with the quadrate by a narrow strand of tissue in which procartilage cells are apparent.* In a 20-mm. larva (fig. 51, C) this rod articulates with the lateral edge of the ethmoid plate, but, although it has grown in a posterior direction, it has not yet joined the quadrate; the two parts become fused in the 30-mm. stage (fig. 51, D). At this stage the palatine section articulates with the cranium in the rostral region. There is a well-marked process on its dorsal edge immediately below the ectethmoid region of the cranium, but no articulation is established here. The hyomandibular is still closely connected with the posterior end of the quadrate, but a definite suture is now visible between the two cartilages. At a late stage the sutures between quadrate and hyomandibular, and quadrate and Meckel's cartilage are replaced by definite articular fissures.

In *Salmo* (STÖHR, 1882; ZANICHELLI, 1909) the upper and lower sections of the arch arise as independent chondrifications, the quadrate section of the upper jaw developing first. The quadrate and hyomandibular are at first closely bound together by procartilage, but no actual fusion takes place. The palatine part does not arise independently as in *Clupea*, but develops as an anterior outgrowth from the quadrate cartilage, its formation being preceded by a strand of procartilage. Anteriorly the palatine acquires a double articulation with the neurocranium; (1) with the side of the rostrum (rostropalatine articulation), and (2) with the base of the ectethmoid region (ethmopalatine articulation) [*cf.* fig. 52, A–E.]

The processes which lead to the development of the mandibular arch in *Gasterosteus* (SWINNERTON, 1902) are very similar to those described in *Salmo*, but there is a marked acceleration in the rate of development of the component elements. The stage at which the upper jaw is represented by a simple quadrate cartilage is either very transitory or is entirely omitted from the ontogeny, the palatine process arising almost simultaneously

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* RYDER (1887, p. 530) describes a similar independent palatine rod in an early larva of *Clupea sapadissima*.

with the quadrate itself. This process subsequently grows anteriorly and establishes an articulation with the rostral region of the cranium ; no ethmopalatine articulation is developed at any stage (fig. 53, A–C).

MACKINTOSH (1923, p. 504) describes the visceral arches of an unhatched embryo of *Sebastes* as being " represented by a relatively extensive but barely differentiated mass of procartilage." I can distinguish several more or less independent elements in the preparations of this stage, but owing to the poor state of preservation, their limits and relations to one another cannot be defined. In a 4·5-mm. larva, the same author (*t.c.*, p. 504) describes the hyomandibular, symplectic and quadrate elements as forming a single plate of cartilage, to which he applies the name " temporale." I am able to detect a somewhat indefinite but true suture between quadrate and hyomandibular at this stage, but in the next stage (5·5 mm.) they are indistinguishably fused as in early larvæ of *Clupea*. No trace of the palatine part of the upper jaw is yet apparent. In a 25-mm. larva the mandibular arch is completely developed, the different elements being separated by articular fissures. Owing to the absence of intermediate stages one cannot say how the palatine section of the palatoquadrate has arisen.*

The development of the mandibular arch in *Amia* and *Lepidosteus* takes place in much the same way as in *Salmo*. The upper and lower parts chondrify independently in a continuous region of procartilage, and the palatine portion of the upper jaw arises as an outgrowth from the earlier developed quadrate part. It is of interest to note that in *Amia* the extreme anterior portion of the palatine cartilage, lying in the region of the future ethmopalatine articulation, chondrifies independently, and is for a time connected with the rest of the palatoquadrate by procartilage (PEHRSON, 1922, p. 8). No fusion of quadrate and hyomandibular takes place in these fishes, nor has such a fusion been described in *Acipenser* or *Polypterus*.

Even in the Selachian fishes we find the mandibular arch developing in much the same way as in the bony fishes, and the palatine part of the upper jaw again arises as an anterior outgrowth (palatine process) from the quadrate part. Instead of articulating with the ectethmoid region of the neurocranium, the anterior ends of the two palatine cartilages bend inwards and either unite directly with one another or are connected by a small median copula (*e.g.*, *Hexanchus*, *Læmargus*).†

In those Selachians in which the orbital (palatobasal) process of the palatoquadrate becomes articulated with the trabecular region of the neurocranium, this articulation appears to be always established at an early stage of the ontogeny. There is never a direct ethmopalatine articulation in adult Selachians, but EDGEWORTH‡ (1925, p. 255)

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* In *Pleuronectes* and *Solea* the quadrate, symplectic and hyomandibular cartilages at first form one triangular mass (BERRILL, 1925).

† The anterior ends of the palatine bars fuse medially in *Acipenser* and *Scaphirhynchus* (SEWERTZOFF, 1923, p. 112).

‡ EDGEWORTH, F. H., " On the Autostylism of Dipnoi and Amphibia," ' J. Anat.,' LIX, pp. 225–264, 26 plates.

has shown that in early stages of *Scyliorhinus* a cartilaginous continuity exists between the palatoquadrate and the antorbital (= ectethmoid) process of the neurocranium; this later degenerates into a ligament. A similar ligamentous connection is found in the adult *Chlamydoselachus* (SEWERTZOFF,* 1923, p. 113).

According to SEWERTZOFF (1897, 1899) the mandibular arch in *Squalus* at first forms a continuous bar of cartilage on each side, which later segments to form the upper and lower jaws. DE BEER (1924*a*) describes a similar process in *Heterodontus*. WIJHE (1922), who has recently re-investigated the development of the visceral arches in *Squalus*, states that the upper and lower sections of the mandibular arch chondrify independently, a conclusion previously arrived at by DOHRN (1884) with regard to this arch in *Pristiurus*, *Scyliorhinus*, and *Centrina*. I have carefully studied preparations of *Squalus* embryos, and am able to confirm WIJHE's statement that in this fish at least the upper and lower jaws arise as separate chondrifications in a continuous bar of procartilage. It is possible that the condition in early embryos of *Heterodontus* is the primitive one, and that this stage has been omitted from the ontogeny of the more specialized Selachians.

To summarize the above, the processes which lead to the formation of the mandibular arch are, on the whole, remarkably similar in all fishes, the chief differences being connected with the development of the palatine section of the upper jaw. The independent chondrification of this part of the palatoquadrate in *Clupea* is undoubtedly a secondary condition. This has not been described in any other bony fish, but an incomplete palatoquadrate cartilage is found in certain Teleosts at sufficiently early stages to warrant the assumption that the anterior part has chondrified independently.†

Owing to the functional replacement of the primitive upper jaw (palatoquadrate) by the bony præmaxillary and maxillary, the cartilaginous upper jaw appears to have undergone a varying amount of reduction in several teleostean genera. This reduction is most marked in *Anguilla*, in which the palatine portion is never developed, although the quadrate part is well marked and arises at an early stage of the ontogeny. In an advanced stage of *Gasterosteus* the middle part of the palatoquadrate is replaced by the rudiment of the palatine ossification, and the palatine and pterygoquadrate sections of the upper jaw, which were at first continuous, are widely separated as in the larval *Clupea*.‡ I have found this condition in advanced larvæ of one or two other Teleosts. It is quite conceivable that in certain of the more specialized§ forms such as the *Clupeidæ*, *Anguil-*

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* SEWERTZOFF, A. N., "The Place of the Cartilaginous Ganoids in the System. . . .," 'J. Morph.,' XXXVIII, pp. 105–145, 4 figs.

† *E.g.*, *Amiurus* (KINDRED, 1919), *Ictalurus* (RYDER, 1887), *Syngnathus* (KINDRED, 1921), *Siphonostoma* and *Hippocampus* (RYDER, 1881*b*). In all these fishes the anterior palatine part is never strictly, independent, but is always connected with the rest of the upper jaw by fibrous or procartilaginous tissue.

‡ The pterygoid portion of the palatoquadrate cartilage is absorbed during the metamorphosis of *Pleuronectes* and *Solea* (BERRILL, 1925, p. 235).

§ The term "specialized" is here intended to apply to the larval forms. The Clupeidæ are admittedly a lowly family of Teleosts, but the larvæ present a number of very specialized features.

lidæ, and *Syngnathidæ*, in which the ontogeny is considerably shortened and the bony jaws are soon developed, the stage at which the palatoquadrate cartilage is complete has been entirely omitted from the ontogenetic record, the middle part of the upper jaw being represented merely by procartilage or fibrous tissue. The retention and early appearance of the quadrate part is explained by the necessity for a strong basis for the support of the lower jaw.

2. *Hyoid Arch.*—The early stages in the development of the hyoid arch in *Clupea* are not known, and in a 5-mm. larva the component elements are already well chondrified

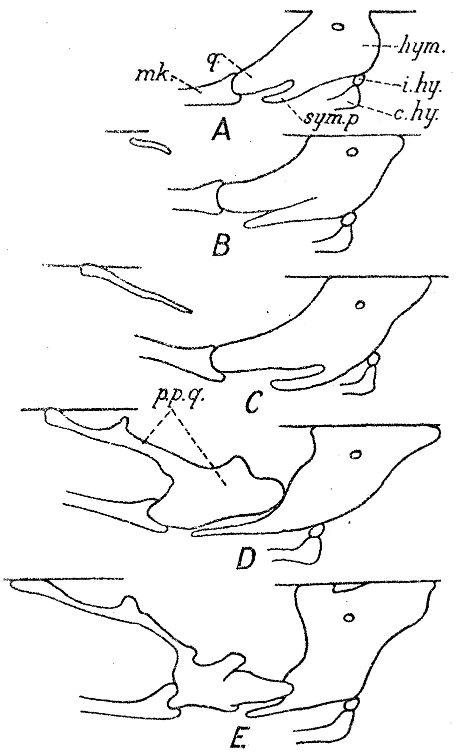

FIG. 51.—Diagrammatic figures of the developing mandibular arch and suspensorial apparatus of *Clupea harengus*; A, 5 mm.; B, 10 mm.; C, 20 mm.; D, 30 mm.; E, 40 mm.

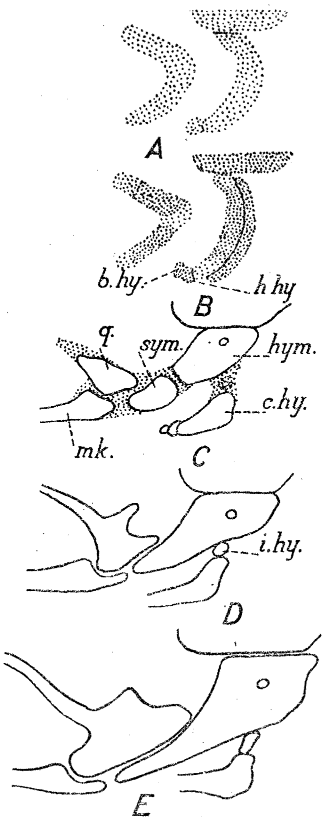

FIG. 52.—The same of *Salmo trutta*; A, B, embryo just hatched; C, 9 mm.; D, 20 mm.; E, about 26 mm. Based on the descriptions of ZANICHELLI (1909), STÖHR (1882), and GAUPP (1906).

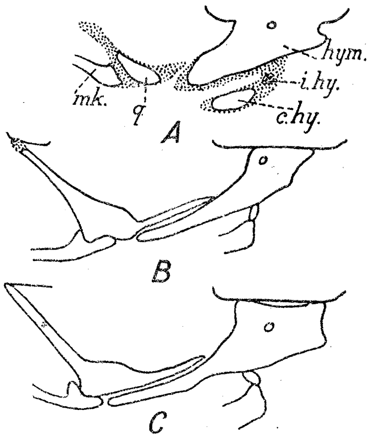

FIG. 53.—The same of *Gasterosteus aculeatus*; A–C, stages I–III (SWINNERTON, 1902).

In all the figures the dotted areas represent procartilage.

and clearly differentiated. The hyomandibular (fig. 51, A, *hym.*) is large and plate-like, and forks ventrally into two processes; the upper and larger of these is the quadrate cartilage (*q.*), which is completely fused with the hyomandibular at this stage, and the lower is the symplectic process (*sym. p.*). A small interhyal* cartilage (*i. hy.*) connects the hyomandibular with the rest of the arch. An independent hypohyal is present at this stage, but the basihyal does not appear until a little later, when it arises as a separate chondrification in the procartilaginous tissue connecting the two hypohyals.

The descriptions of the development of this arch in *Salmo* given by Stöhr (1882) and Zanichelli (1909) differ in several respects. In all discussions concerning the visceral arches of fishes, *Salmo* is generally accepted as typifying the teleostean condition, and for this reason it will be necessary to summarize briefly the accounts of both authors. Zanichelli's work appears to have been overlooked by nearly all workers on the fish chondrocranium.

Zanichelli (1909, pp. 247–249) describes the hyoid arch as beginning to segment, while the mandibular arch is still quite simple. It is at first composed of a pair of simple procartilaginous bars, the ventral ends of which are joined by a rudimentary basihyal (fig. 52, A). Each of these bars soon splits vertically into two parallel and contiguous rods, the anterior and thicker of which is connected with the basihyal by a small element, the hypohyal, which has been differentiated from the distal end of the original bar (fig. 52, B). The anterior rod is the hyomandibular, and the thinner posterior one becomes the ceratohyal. As soon as the split has occurred the hyomandibular moves forward and becomes associated with the mandibular arch, retaining, however, its original connection with the otic region of the neurocranium. The upper end of the ceratohyal is carried away from the cranium during this movement, and this element moves forward with the hyomandibular, becoming connected ventrally with the hypohyal. At a slightly later stage the interhyal appears, and is said to be differentiated from the upper end of the ceratohyal.

Stöhr (1882) describes the first appearance of the hyoid arch as a pair of procartilaginous tracts in which three isolated areas of cartilage are soon differentiated, representing respectively the hyomandibular, symplectic and ceratohyal. The symplectic cartilage lies close behind the quadrate and very soon fuses with the distal end of the hyomandibular. The interhyal is said to arise from the upper end of the ceratohyal, and the hypohyal arises as an independent chondrification at the lower end of the same element. The basihyal is said to be segmented off from the anterior end of the primary copula which develops between the lower ends of the first branchial arch and grows forward between the two halves of the hyoid arch.

The hyoid arch of *Gasterosteus* develops in much the same way as that of the Salmon (as described by Stöhr), and the hyomandibular at first forks ventrally into two procartilaginous processes each with a zone of true cartilage (fig. 53, A). The symplectic, however, arises in connection with the hyomandibular, and is never independent. The basihyal chondrifies independently (Swinnerton, 1902). In *Sebastes* (Mackintosh, 1923) the

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* I have used the term "interhyal" throughout this paper, as it seems to be at once suitable and more appropriate than "stylohyal," the use of which implies a homology with the element of that name in the hyoid arch of the Mammal, a homology which is by no means definitely established.

symplectic cartilage again develops in continuity with the hyomandibular, which in a 4·5-mm. larva is separated from the ceratohyal by an area of procartilage in which the interhyal is shortly afterwards differentiated. No hypohyal is developed at any stage.

In *Amia* (Pehrson, 1922) the different elements of the arch arise as separate chondrifications in a continuous tract of procartilage, which merges insensibly into the procartilaginous rudiment of the auditory capsule. The interhyal and hypohyal arise as independent elements in the tissue surrounding the upper and lower ends of the ceratohyal. The symplectic is never independent, and forms a process of the hyomandibular from the first (fig. 54, A-D). The processes in *Lepidosteus* are almost exactly parallel. Even when fully chondrified, the different elements of the hyoid arch are for some time closely connected with one another by richly cellular, darker staining procartilage, such as has been described in *Anguilla*, and the definitive articular fissures, formed by the interposition of connective tissue, are not formed until a comparatively late stage (Veit, 1911).

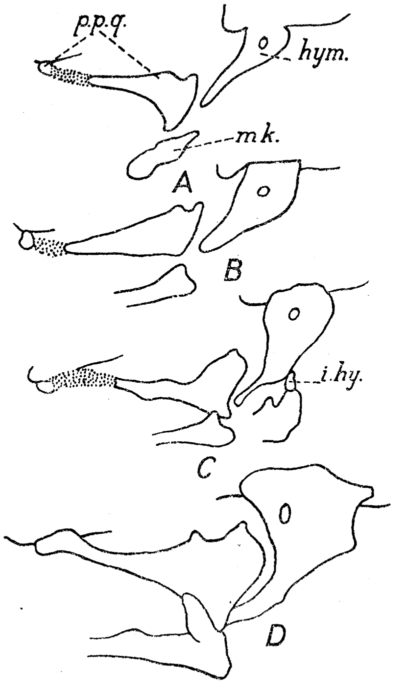

Fig. 54.—The same of *Amia calva*; A, 9·3 mm.; B, 9·2–9·9 mm.; C, 10–11 mm.; D, 19·5 mm. After Pehrson (1921).

In all the figures the dotted areas represent procartilage.

The "symplectic" apparently arises separately in *Acipenser*, and is retained as an independent element in the adult.

The different parts of the hyoid arch in the Selachians may arise, either as independent chondrifications, or through the segmentation of a primarily continuous bar of cartilage. These two methods of development occurring within the same group have been previously noticed in connection with the mandibular arch. Each of the visceral arches of fishes was probably primarily represented by a simple hoop of cartilage, or by two half-hoops connected ventrally, and there is little doubt that these became segmented at an early period of their history. The segmentation was an adaptive arrangement to facilitate the movements connected with respiration. The stage at which the hyoid arch forms a pair of simple unsegmented cartilaginous rods has been dropped out of the ontogeny of the more specialized Selachians.

C. *The suspension of the jaws in fishes, and the homologies of certain elements in the mandibular and hyoid arches.*—Most workers on the visceral arches have followed Gegenbaur (1872) in assuming that the form of the mandibular arch in recent Selachians is a primitive one, and that the palatoquadrate represents an element which combines the epal and pharyngeal cartilages, and which has never been segmented. In the same way, Meckel's cartilage is regarded as being composed of undifferentiated cerato- and hypomandibular elements. Others have concluded that the mandibular arch of the ancestors of living fishes contained the four typical elements which make up each branchial arch, and that the condition in Selachians has been brought about by the reduction, or more generally the complete loss of the pharyngeal and hypal elements. SEWERTZOFF (1923) has recently discussed the question at some length, and adopts the latter view. He has described an independent pharyngomandibular cartilage in the Palæopterygian *Scaphirhynchus*, and compares it with the orbital (palatobasal) process of the Selachian palatoquadrate. WHITE* has described a small, independent cartilage lying at the anterior end of MECKEL'S cartilage in *Hexanchus* and *Laemargus*, and this is regarded by SEWERTZOFF as a remnant of the hypal element of the mandibular arch, an element which has been lost in nearly all other fishes.† The development of this arch in the different groups of fishes throws little light on this problem.

In considering the primitive region of articulation of the mandibular arch with the neurocranium, we are again faced with two opposing views, each of which had attracted a number of adherents. Many follow GEGENBAUR in regarding this place of articulation as being in the postorbital region, and assume, therefore, that the condition found among living sharks in the Notidanidæ, where the large otic process of the palatoquadrate articulates with the postorbital process of the neurocranium, is a primitive one (fig. 55, A). Others concluded that the upper part of the arch primarily articulated with the trabecular region of the neurocranium through the orbital‡ process of the palatoquadrate. If the postorbital articulation is regarded as a primitive one, then the whole of the palatoquadrate anterior to this must be regarded as an entirely new formation which has grown forward from the upper end of the original mandibular arch.

SEWERTZOFF (1923), in a most instructive paper, has produced strong evidence in favour of the view that the articulation of the orbital process is the more primitive, and my own researches have led me to the same conclusion.

An orbital process is developed to some extent in nearly all Sharks, although it is somewhat reduced in some of the more specialized forms, and is frequently very small in the Rays. In the adult *Heterodontus* (fig. 55, C), however, this process is represented merely by a slight eminence on the upper edge of the palatoquadrate, but is well developed during the embryonic stages (fig. 55, B) [*cf.* DE BEER, 1924*a*, p. 43]. In all those Selachians in which the development of the jaws has been studied, the orbital process appears at an early stage, and from the first is united by dense tissue with the trabecula.

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* 'Anat. Anz.,' XI, 1895, p. 57.

† ALLIS ('J. Anat.,' LVIII, 1923, p. 48) concludes that the palatine process of the Selachian palatoquadrate, *i.e.*, that part of the upper jaw anterior to the orbital process, represents the epal element of the arch, while the trabecular cartilage of the neurocranium represents the pharyngomandibular.

‡ The two processes which may be developed to a greater or lesser extent on the upper edge of the palatoquadrate of Selachians have received a number of names. The more anterior one has been called the palatine, palatal, ethmopalatine, trabecular, orbital, or palatobasal process; the posterior has been named quadratic, otic, metapterygoid, or pedicular process, or simply the pedicle. I have adhered to the nomenclature of ALLIS (1914).

The otic process of the palatoquadrate, on the other hand, is entirely wanting in a large number of Selachians, and, when present, arises at a comparatively late stage. I am convinced that the postorbital articulation of the Notidanidæ, which may be correlated with the large size of the gape and the strength of the jaws in these fishes, is a secondary feature as suggested by HUXLEY (1876, p. 44).*

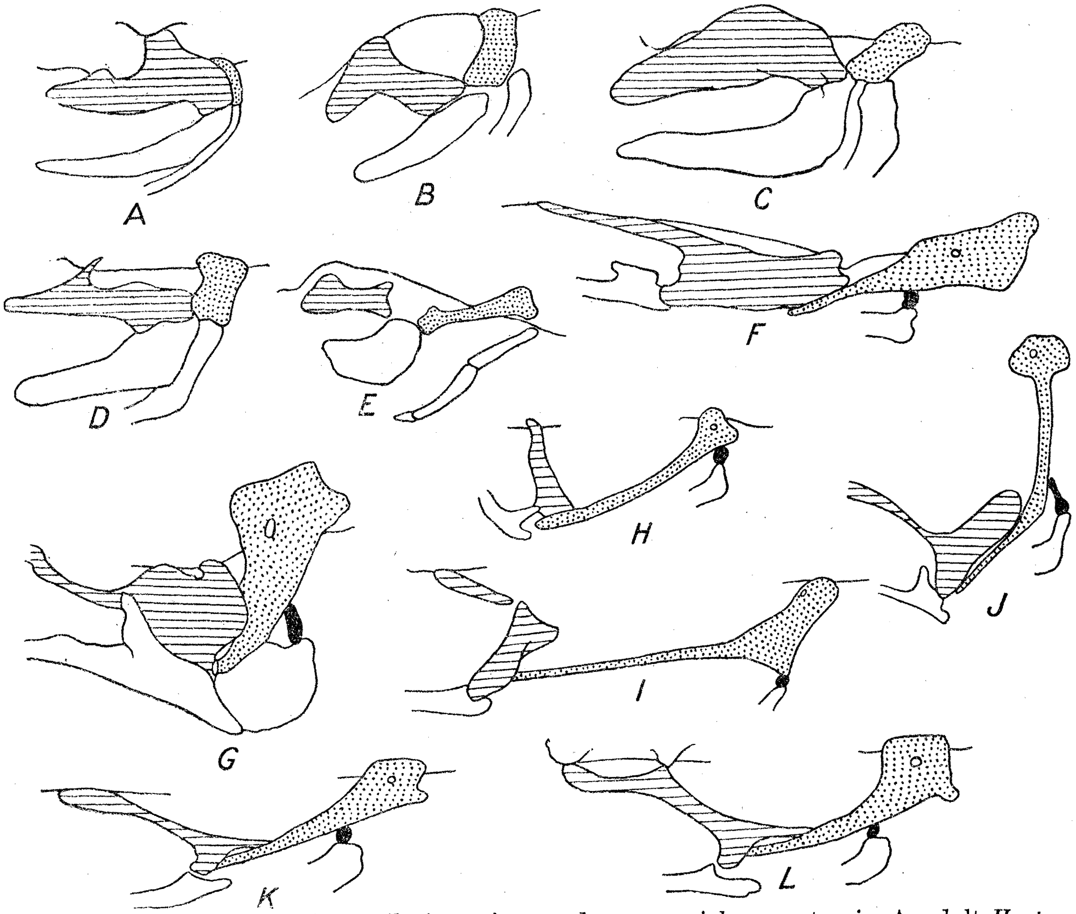

FIG. 55.—Diagrams illustrating the cartilaginous jaws and suspensorial apparatus in A, adult *Heptanchus* (after GOODRICH); B, 45 mm. embryo of *Heterodontus* (after DE BEER); C, adult *Heterodontus*; D, adult *Squatina* (after GEGENBAUR); E, adult *Raia*; F, 20·5 mm. *Lepidosteus* (after VEIT); G, 31·5–34·5 mm. *Amia* (after PEHRSON); H, 7 mm. *Gambusia* (after RYDER); I, 14 mm. *Siphonostoma*; J, 25 mm. *Sebastes* (after MACKINTOSH); K, 11 mm. *Esox*; L, 17–25 mm. *Esox* (after WALTHER).

░ = Hyomandibular; ☐ = Ceratohyal and Meckel's cartilage; ▤ = palatoquadrate; ■ = interhyal.

A somewhat similar postorbital articulation is found in the Palæozoic Pleuropterygii, Acanthodii, and Ichthyotomi. REGAN† has shown that in two suborders of the Euselachii,

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* HUXLEY, T. H., "Contributions to Morphology. Ichthyopsida. I. On *Ceratodus forsteri*, with Observations on the Classification of Fishes," 'Proc. Zool. Soc.,' 1876, pp. 24–58, 11 figs.

† REGAN, C. T., "A Classification of the Selachian Fishes," 'Proc. Zool. Soc.,' 1906, pp. 722–758, 10 figs.

the Notidanoids and the Squaloids, there are families without (*e.g.*, Chlamydoselachidæ, Heterodontidæ, Squalidæ), and families with (*e.g.*, Hexanchidæ, Hybodontidæ) a post-orbital articulation; he regards the former condition as the primitive one.

The position of the articulation of the orbital process with the neurocranium varies somewhat in different Selachians. In the Notidanidæ it lies in the orbitotemporal region, but in more specialized forms it tends to occupy a more anterior position, and in *Mustelus* and *Squatina* (fig. 55D), lies in the ethmoid region of the neurocranium.

In all the Selachians, with the exception of the Holocephali, the anterior ends of the two palatoquadrate bars are united in a symphysis below or a little behind the ethmoid region.* In the bony fishes, except *Acipenser* and *Scaphirhynchus*, the upper jaws have become widely separated anteriorly, and at the same time the whole mandibular arch appears to have been thrust somewhat forward. This anterior movement of the jaws appears to be recapitulated to a certain extent in the ontogeny of *Salmo*. According to ZANICHELLI (1909, p. 243), in a very young Trout embryo the palatoquadrate cartilages curve inwards anteriorly, and the horseshoe-shaped mouth lies on the lower surface of the head and closely resembles that of some adult Selachians. This position is said to be retained for some time after hatching, and then the mouth commences to move forward and soon acquires the terminal position found in the adult Trout.

It seems probable that the orbital process of Selachians is represented in bony fishes by that process or ridge of cartilage on the upper edge of the palatine cartilage, which usually forms the posterior boundary of the surface by which the palatine articulates with the ectethmoid region of the neurocranium. Such a process is well developed in the larval *Salmo*, and acquires an early connection with the base of the ectethmoid cartilage. In the larval *Clupea* (WELLS, 1923, figs. 9–10) this process is even more marked, but, although it projects towards the ectethmoid, never becomes articulated in this region. In some of the more specialized Teleosts (*e.g.*, *Gasterosteus*, *Syngnathus*) no trace of this process is apparent, and the ethmopalatine articulation has disappeared.

That part of the Selachian palatoquadrate lying anterior (medial) to the orbital process ("Oberkieferfortsatz" of German authors), appears to have been entirely lost in bony fishes. The portion of the palatine cartilage anterior to the ethmopalatine articulation in *Amia*, *Lepidosteus* and the Teleosts, must, therefore, be regarded as a new formation, and this view is supported by the fact that this part of the palatine chondrifies independently in *Amia* and certain Teleosts. Further, in view of the fact that in *Amia*, *Lepidosteus*, and in several Teleosts, this part of the palatine is continuous with the ethmoid region of the neurocranium during the early stages of development, it is possible that it has been derived from the cartilage of the cranium itself and has become secondarily detached. LUNDBORG† has shown that in certain bony fishes the cell

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* Their anterior ends are linked together by a small median copula in certain sharks.

† LUNDBORG, H., "Studien über die Betheiligung des Ektoderms . . . . ," 'Morph. Jahrb.,' XXVII, 1899, pp. 242–262, pls. XI–XII, 6 text-figs.

material of the anterior part of the palatine cartilage can be demonstrated to be derived from the ethmoid plate.

SWINNERTON (1902) distinguished three types of articulation of the palatine cartilage with the ethmoid region in Neopterygian fishes, which he named "Panartete," "Disartete" and "Acrartete." A study of the conditions existing in a number of embryo and larval Teleosts has convinced me that these types are not of fundamental importance, and represent modifications connected with the shape of the cranium and the general form and size of the jaws. In an 11-mm. *Esox* (WALTHER, 1883, pl. III, figs. 1, 7) the palatine has an elongate articulation with the ventrolateral edge of the ethmoid plate (fig. 55, K), but at a later stage the articulation is both of the rostropalatine and ethmopalatine type, and corresponds to the condition described by SWINNERTON as disartete (fig. 55, L).

Nearly all those forms in which the ethmopalatine articulation has been lost, and the palatine cartilage is joined solely to the rostral region, are characterized by the possession of a more or less elongate ethmoid region, and it is this condition which seems to have been the chief cause of the loss of the more posterior articulation. Such an elongation is most marked in the Syngnathidæ, in which the whole mandibular arch has been carried so far forward that it is situated entirely in front of the ectethmoid cartilages, which lie above the middle of the symplectic (fig. 55, I).

In *Gymnarchus*, of the family Mormyridæ, the anterior part of the palatoquadrate becomes completely fused with the ventral surface of the neurocranium, a condition which is established at a comparatively early stage of development (ASSHETON, 1907).

In *Lepidosteus* the palatoquadrate cartilage has a second articulation with the neurocranium in the posterior part of the orbitotemporal region (fig. 55, F), through the junction of the so-called pedicular process or pedicle with the basipterygoid process of the trabecular cartilage. GAUPP (1906) and SWINNERTON (1902) compare this articulation with the orbital or palatobasal articulation of Selachians, and regard the condition in *Lepidosteus* as a primitive one. I agree with VEIT (1911), REGAN,* and others, however, in regarding this articulation as quite secondary, and believe that it has been acquired solely to relieve the strain on the suspensorial apparatus brought about by the great increase in size and length of the lower jaw in this fish. The articulation of the orbital process of the palatoquadrate with the cranium is established at an early stage in Selachians, whereas this palatobasal articulation of *Lepidosteus* is acquired comparatively late in the ontogeny. The so-called pedicular process of *Amia* and certain of the lower Teleosts, which is compared by SWINNERTON with the process of the same name in *Lepidosteus*, also develops at a comparatively late stage (*cf.* figs. 52, 54). The same author lays great stress on the fact that the metapterygoid region of the palatoquadrate cartilage becomes progressively reduced as we pass from the lower Teleosts to the more specialized forms, but this reduction seems to be connected

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* REGAN, C. T., "The Skeleton of *Lepidosteus*, with remarks on the Origin and Evolution of the lower Neopterygian Fishes," 'Proc. Zool. Soc.,' 1923, pp. 445–461, 8 figs.

merely with the general reduction in the size of the jaws in those specialized Teleosts which he studied.

The nature and homologies of the hyomandibular cartilage in the different groups of fishes has been for many years the subject of much investigation, and one about which there is a great difference of opinion. The question of its homologies has been discussed at great length by ALLIS (1915, 1918), and has also been dealt with recently by SCHMALHAUSEN (1923) and DE BEER (1924*b*).

Commencing with the Selachians, there is little doubt that the hyomandibular of the Sharks (Pleurotremata) represents the epal element of the hyoid arch. This conclusion, which is based on a number of facts concerning the relations of the hyomandibular to the neurocranium, and to the associated muscles, nerves and blood-vessels, is further supported by the fact that an independent pharyngohyal cartilage has been observed in the embryonic or adult stages of *Stegostoma, Galeus, Mustelus* and other genera (LUTHER, 1909, p. 13* ; SEWERTZOFF, 1923). ALLIS (1915), while he agrees with this conclusion, regards the hyomandibular of the Rays (Hypotremata) as the pharyngeal element. These fishes, however, present a number of features which show that they are clearly modified and specialized Sharks, and it is scarcely conceivable that the articulation of the hyoid arch with the cranium should be through a different element in the two groups. Further, the presence of a rudimentary pharyngohyal in *Trygon* and *Torpedo* (SEWERTZOFF, 1923) suggests that in the Rays the hyomandibular is also the epal element, and is strictly homologous with the hyomandibular of the Sharks.

The presence of an independent pharyngohyal in *Chimæra* (SEWERTZOFF, 1923) and *Callorhynchus* (SCHAUINSLAND, 1903) makes it clear that the hyomandibular is a true epihyal in the Holocephali. As pointed out by REGAN† (1910, p. 126), the presence of this element also shows that the autostyly of these fishes cannot be a modified hyostyly as has been suggested by some authors.

In all Selachians the hyomandibular articulates with the ventral surface of the auditory capsule, medial to the hyomandibular muscle and jugular vein (fig. 56, A). In the class Pisces, on the other hand, the articulation is always with the lateral edge of the capsule, and external to both the muscle and the vein. In all fishes the upper ends of the branchial arches come into contact with the cranium medial to the jugular vein, and, since there is every reason to assume that the hyoid arch was originally essentially similar to the branchial arches, the condition in the Selachians may be regarded as the more primitive.

POLLARD (1895*b*, p. 23) first expressed doubt as to the homology of the hyomandibular in the two groups of fishes, and concluded that that of the Pisces represented a part of the mandibular arch, and that the interhyal of these fishes was the true homologue of the Selachian hyomandibular. He compared the hyomandibular of the bony fishes

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* LUTHER, A., "Beiträge zur Kenntnis von Muskulatur und Skelett des Kopfes des Haies *Stegostoma* . . . . ," 'Acta. Soc. Sci. Fenn.,' XXXVII, No. 6, 60 pp., 36 text-figs.

† 'Proc. Intern. Zool. Congress,' Boston, 1907, p. 837 (1912).

with the otic process of *Heptanchus*. Since his descriptions of the relations of the cartilage to the spiracle and to the facial nerve are, in several respects, inaccurate, his conclusions cannot be fully accepted.

Allis (1915, 1918) also concludes that the hyomandibular is not homologous in the two groups, and regards the interhyal of the bony fishes as representing the epal element of the hyoid arch. He attributes a double origin to the hyomandibular of the Pisces, the anterior head being an " anterior branchial ray " of the hyoid arch, and the posterior head an extrahyal element.

Schmalhausen (1923) and De Beer (1924*b*) both agree in tracing the hyomandibular of the Selachians and of the Pisces from an intermediate form which had a double articulation with the neurocranium, an inner one medial to the hyomandibular muscle and jugular vein, and an outer one on the edge of the auditory capsule. Schmalhausen regards the hyomandibular of both classes as an epihyal, and assumes that the condition in the Pisces has been brought about by a change in the position of the articulation. De Beer does not accept this view, and holds that the hyomandibular of Selachians is a true hyomandibular, and that of the Teleosts and *Amia* is said to be a compound of an interarcual cartilage and a " processus oticus hyomandibularis," the latter being a modified extrahyal.

Most authors, in discussing this question, appear to have started with the assumption that the hyostylic suspensorium of bony fishes has been derived directly from a condition similar to that found in the Euselachii; on account of the difference in the relations of the associated muscles and blood-vessels in the two groups, they find it impossible to accept the view that the hyomandibular is homologous in the Euselachii and the Pisces. Since, however, the hyostyly of the Euselachii and of the Pisces has almost certainly been acquired independently, this argument becomes invalid.

My own researches have led me to conclude without hesitation that a part at least of the hyomandibular of bony fishes represents the epal element of the hyoid arch, and that the upper articular portion may be a new structure. This upper portion may possibly have been derived from the cartilage of the neurocranium itself, a view which is supported by the partial continuity of the cartilage of the hyomandibular and that of the auditory capsule during the early developmental stages of *Amia, Lepidosteus*, and certain Teleosts.

The complex origin attributed to the hyomandibular of bony fishes by Allis and De Beer does not seem to me to be supported by a study of its development, and the suggested component parts are largely hypothetical. De Beer (1924*b*) attributes the lateral position of the articulation in bony fishes to the adoption by the hyomandibular of the function of supporting the bony operculum, which lies wholly external to the branchial arches. This support of the operculum, however, must be a secondary condition, and I do not see how it can have affected the position taken up by the articular end of the hyomandibular.

Schmalhausen (1923, p. 534, fig. 1) describes and figures the relations of the upper end of the hyoid arch to the cranium in a young *Ceratodus*. The articulation of the hyomandibular is of the bony fish type, but a small, independent cartilaginous element is also developed, which lies medial to the jugular vein and hyomandibular muscle, and is connected by a ligament with the ventral surface of the auditory capsule.* DE BEER (1924*b*, p. 335) regards this element as the true hyomandibular, and the structure articulating with the outer edge of the capsule as corresponding to his " processus oticus hyomandibularis." I have not studied preparations of developing *Ceratodus*, but suggest that the small independent cartilage may be a pharyngohyal.†

The relations of the hyoideomandibular branch of the facial nerve and the hyomandibular cartilage differ considerably in the various groups of fishes. In the Euselachii this ramus passes posteriorly dorsal to and outside the cartilage, a condition which is probably primitive (fig. 56, A). In *Polypterus* the nerve divides into two branches before reaching the hyomandibular ; the mandibular branch passes in front of the cartilage, the hyoidean ramus behind it. In *Acipenser* the nerve passes outwards posterior to and below the hyomandibular. In all Neopterygian fishes it pierces the cartilage (fig. 56, B).

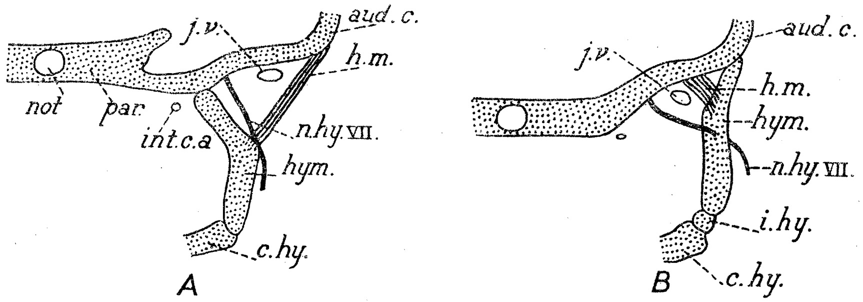

FIG. 56.—Diagrams illustrating the relations of the hyomandibular to the neurocranium, etc., in (A) Euselachii, (B) Neopterygian fishes.

It is probable that when the hyostylic type of suspensorium was acquired by the bony fishes the nerve at first ran outwards behind the hyomandibular cartilage, as it does in the Euselachii and in *Acipenser*. The condition found in the Neopterygii has arisen, not through the perforation of the cartilage by the nerve, but by the surrounding of the nerve through the posterior extension of the cartilage. EDGEWORTH (1911, p. 209) has shown that in *Amia*, *Lepidosteus*, and *Salmo*, the hyoideomandibular ramus at first " winds round the hyoid bar, and subsequently pierces the hyomandibular owing to chondrification spreading round it."‡

In *Clupea*, *Anguilla*, *Sebastes*, and other Teleosts, the hyomandibular is, from the time of its first appearance, closely connected or actually fused with the hinder part

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* The development of the quadrate and epihyal cartilages of *Ceratodus* has been described in detail by EDGEWORTH (' Q. Journ. Micr. Sci.,' LXVII, 1923, pp. 359–368, figs. 31–39).

† *Cf.* SCHMALHAUSEN, 1923, p. 534.

‡ In *Pleuronectes* and *Solea* this nerve ramus at first passes round the posterior side of the cartilage ; in the second stage it " becomes enveloped in that cartilage, and the foramen thus formed migrates some way towards the anterior side " (BERRILL, 1925, p. 235).

of the quadrate cartilage. In *Salmo* (ZANICHELLI, 1909), on the other hand, this cartilage appears to be at first a part of the definitive hyoid arch, but soon moves anteriorly and joins the quadrate. There appears to have been a general acceleration in the rate of development of the component elements of the jaws and suspensorium of such fishes as the Herring and the Stickleback, and the stage at which the hyomandibular forms a part of the hyoid arch proper is either very transitory or is altogether omitted from the ontogeny. Since the larvæ of these fishes begin to move actively about and to use their jaws for obtaining food soon after hatching, and since the hyomandibular supports the operculum, and, in the absence or incomplete development of the palatoquadrate, the lower jaw also, the reason for this rapid completion of the cartilages of the jaws and suspensorium becomes clear.

Such an acceleration is particularly marked in the larval *Anguilla*, in which the cartilaginous mandibular and hyoid arches are soon developed, and, in addition, toothed maxillary and dentary bones are present at a stage when the cartilaginous neurocranium is still very incomplete.

ALLIS (1915, p. 620) concludes that the symplectic of bony fishes is "probably a primarily independent cartilage, and is possibly a hypertrophied middle one or ones of the branchial rays of the mandibular arch." This conclusion does not seem to me a probable one, and is not supported by embryological evidence. True, STÖHR (1882) has described the symplectic as chondrifying independently in *Salmo* and later becoming fused with the hyomandibular, but this is not confirmed by ZANICHELLI (1909), nor does the symplectic cartilage have an independent origin in any other Teleost or in *Amia* or *Lepidosteus*. In the Palæopterygii (*Acipenser*, *Scaphirhynchus*, *Polyodon*) there is an independent symplectic, but this is segmented off from the hyomandibular and does not chondrify independently. I regard the symplectic cartilage of bony fishes as a process or ventral prolongation of the hyomandibular, which runs below the hinder end of the quadrate cartilage and provides a strong basis for the articulation of the two elements.

It is of interest to note that in those Teleosts with a small, anteriorly situated mouth, the reduction in the size of the gape is nearly always accomplished by a corresponding elongation of the symplectic cartilage. In *Gasterosteus* (fig. 53, C) the jaws are of moderate size and the symplectic process is fairly elongate; in *Gambusia* (fig. 55, H), with a smaller mouth, this process is correspondingly longer; and in the Syngnathidæ (fig. 55, I) the symplectic has become very elongate, and the comparatively minute jaws have been carried forward to the end of the tube-like snout. On the other hand, in *Anguilla* and *Clupea*, in which the gape is fairly large, the symplectic process is comparatively short.

The interhyal element of the hyoid arch may be regarded as a new structure, which has been developed in correlation with the need for a stronger suspensorium for the remainder of the hyoid arch after the hyomandibular had moved forward and become associated with the jaws. The fact that in *Amia* and *Lepidosteus* this element arises as an independent chondrification, suggests that it developed primarily as a separate cartilage in the ligament connecting the hyomandibular with the ceratohyal. In *Salmo*, however, it is segmented off from the upper end of the ceratohyal (STÖHR, 1882; ZANICHELLI, 1909).

No interhyal is present at any stage of development in *Gymnarchus*.

SUMMARY.

Development of the Chondrocranium of Anguilla vulgaris.

Three stages in the development of the chondrocranium prior to the metamorphosis are fully described, and one stage during the metamorphosis is briefly dealt with.

The chondrocranium is typically tropibasic.

There is no rostral cartilage at any stage. The ectethmoid cartilages arise in a 17-mm. larva as dorsal upgrowths from the ethmoid plate. The oblique eye-muscles are connected with the hinder end of the mesethmoid cartilage, and no anterior eye-muscle canal is developed. The ophthalmic branch of the trigeminal nerve does not pierce the ectethmoid.

The supraorbital bands do not arise as outgrowths from the auditory capsules. No epiphysial bar is present at any stage, nor is any cartilaginous roof developed in the anterior part of the cranium.

The trabeculæ are already fused with one another in a 5-mm. larva, and pass imperceptibly into the parachordals. A very small basicranial fenestra is present in the earlier stages, which subsequently enlarges and is divided into two by a bridge of cartilage. The surrounding cartilages are modified in connection with the internal carotids and other arteries.

The rectus eye-muscles are connected with the hinder end of the trabecula communis, and no myodome is developed.

A trigemino-facialis chamber is present in the earlier stages but is later suppressed. The branches of the trigeminal nerve never pass out through definite foramina in the cranium.

The cavity of the auditory capsule opens directly into the cranial cavity, no medial wall being developed. Only the lateral and posterior semicircular septa become chondrified. The base of the capsule is at first connected with the parachordal by a single, anterior commissure of cartilage, the posterior commissure appearing later.

The parachordals of a 5-mm. larva cannot be divided into mesotic and occipital sections. These cartilages gradually meet above the notochord during development. There is a marked difference in the rate of growth of the medial and lateral parts of the cranium during the earlier stages.

The notochord never undergoes any reduction in length, but continues to grow throughout the præmetamorphosis development.

None of the occipital nerves pierce the lateral walls of the occipital region, and only a single pair exits above the hinder ends of the parachordals.

The first part of the synotic tectum to develop is formed largely from the occipital processes; the more anterior portion arises a little later through the medial fusion of the auditory capsules above the brain.

During the metamorphosis, the mesethmoid cartilage, parts of the ethmoid plate, and the greater part of the ectethmoids, supraorbital bands, and trabecula communis entirely disappear.

The various elements of the visceral arches are separated from the first by a thin layer of richly cellular tissue; during the metamorphosis definite articular fissures appear.

The upper part of the mandibular arch is never developed, only the quadrate portion being present.

The hyomandibular is never fused with the auditory capsule or with the quadrate cartilage; its lower end grows out into a short symplectic process. The opercular process arises independently of the hyomandibular. No hypohyals are developed.

The maxillary and dentary bones are already present in a 5-mm. larva, and are provided with teeth. Separate præmaxillaries arise at a much later stage.

In the comparative section of this paper, the subjects described and discussed are briefly indicated in the heading of each section, and it is difficult to epitomise the results more briefly than has been done in the text itself. Only a few of the more important conclusions are therefore summarized here.

The ectethmoid cartilages of bony fishes arise primarily as outgrowths from the ethmoid plate, but may chondrify independently in certain Teleosts. They correspond to the lateral ethmoid wings of the Selachian cranium.

The single anterior eye-muscle canal of *Salmo* and other Teleosts has been derived from the short, paired canals of such a fish as *Amia*. In those Teleosts with comparatively small eyes, the oblique eye-muscles do not penetrate the mesethmoid cartilage.

The relations of the olfactory lobes, nerves, and nasal organs in bony fishes have been derived directly from the "Cyclostome" condition, in which the lobe lay between the brain and the nasal organ, within the cranial cavity, and was closely applied to both.

The polar cartilages are not morphologically independent elements.

The "horizontal" and "vertical" types of relationship between trabeculæ and parachordals are connected with the time of appearance of the trabeculæ and the degree of the mesocephalic flexure of the head.

A basicranial fenestra is present in the chondrocranium of all bony fishes.

The fusion of the internal carotid arteries in the larval *Anguilla*, and the formation of a separate carotid foramen, appear to be unique among larval Teleosts. The relations of these and associated arteries to the cranial floor is somewhat similar to those in embryo *Squalus*.

No part of the myodome is derived from the cranial cavity proper.

There is no interorbital septum in *Lepidosteus*. The septum of bony fishes was derived primarily from material which originally formed the inner walls of the orbits in the platybasic cranium.

A definitive trigemino-facialis chamber, which has been described in early *Leptocephalus* larvæ, is not present in any other embryo or larval Teleosts. Such a chamber is well developed in *Amia* and *Lepidosteus*.

The first connection of the auditory capsule with the parachordal takes place through the anterior basicapsular commissure in bony fishes, and the posterior commissure arises considerably later.

In many Teleosts a part of the parachordal cartilage takes part in the formation of the floor of the auditory capsule. No medial wall is ever developed in the capsule of Teleosts.

The median rostral cartilage of certain Teleosts has been formed by the fusion of the paired præmaxillary cartilages, which probably correspond to the anterior upper labial cartilages of Selachians.

The development of the mandibular arch takes place in much the same manner in all fishes, the chief differences being connected with the formation of the palatine portion of the palatoquadrate. The upper and lower sections of the mandibular arch arise independently in *Squalus*.

The articulation of the orbital process of the Selachian palatoquadrate with the trabecular region of the neurocranium is the primitive one, and represents the original dorsal end of the mandibular arch. The otic articulation in the Notidanidæ is secondary.

The so-called palatobasal articulation of the palatoquadrate with the trabecular region in *Lepidosteus* is a secondary condition.

The hyomandibular (or at least a part of it) represents the epal element of the hyoid arch in the Selachians and in the living members of the class Pisces. The upper articular part of the hyomandibular of bony fishes is probably a new structure, and may have been derived from the cartilage of the neurocranium itself.

The symplectic cartilage is not a morphologically independent element, but represents a process of the hyomandibular which has become secondarily segmented off in certain fishes.

The interhyal of bony fishes is a new element, and probably one which has developed in the ligament connecting the hyomandibular with the remainder of the hyoid arch.

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KEY TO LETTERING USED IN THE TEXT-FIGURES.

a.bl., vesicle of air-bladder; *a.lab.*, auditory labyrinth; *aud.c.*, auditory capsule *b.br.* 1–4, first to fourth basibranchial cartilages; *b.fen.* 1, *b.fen.* 2, anterior and posterior basicapsular fenestræ; *b.hy.*, basihyal cartilage; *bas.fen.*, basicapsular fenestra; *bas.fs.*, basicapsular fissure; *br.*, brain; *buc.c.*, buccal cavity; *c.br.* 1–5, first to fifth ceratobranchial cartilages; *c.hy.*, ceratohyal cartilage; *c.t.*, canine tooth; *cr.c.*, cranial cavity; *dt.*, dentary bone; *e.*, eye; *e.br.* 1–4, first to fourth epibranchial cartilages; *e.p.*, ethmoid plate; *e.p.a.*, efferent pseudobranchial artery; *ect.eth.*, ectethmoid cartilage; *ext.r.m.*, external rectus eye-muscles; *f.*VII, facial foramen; *f.*IX, foramen of glossopharyngeal nerve; *f.*X, jugular foramen; *f.hy.*VII, foramen of hyoideomandibular ramus of facial nerve; *f.mag.*, foramen magnum; *f.op.*VII, foramen of ophthalmic branch of facial nerve; *f.op.a.*, foramen of ophthalmic artery; *f.ot.*VII, foramen of otic branch of facial nerve; *f.pal.*VII, foramen of palatine branch of facial nerve; *fs. par.*, interparachordal fissure; *gn.g.*, geniculate ganglion; *gs.g.*, gasserion ganglion; *h.br.* 1–4, first to fourth hypobranchial cartilages; *h.hy.*, hypohyal cartilage; *hym.*, hyomandibular cartilage; *hyp.*, hypophysis; *i.hy.*, interhyal cartilage; *i.mx.*V, incisure for maxillo-mandibulary ramus of trigeminal nerve; *i.o.m.*, inferior oblique eye-muscles; *i.op.*V, incisure for ophthalmic ramus of trigeminal nerve; *i.r.m.*, inferior rectus eye-muscles; *i.sp.*, interorbital septum; *int.c.a.*, internal carotid artery; *int.r.m.*, internal rectus eye-muscles; *j.v.*, jugular vein; *l.s.c.*, lateral semicircular canal; *l.s.sp.*, lateral semicircular septum; *lt.g.*, lateralis ganglion; *m.eth.*, mesethmoid cartilage; *m.eth.b.*, mesethmoid bone; *m.eth.pr.*, process of mesethmoid cartilage for attachment of oblique eye-muscles; *mk.*, Meckel's cartilage; *mx.*, maxillary bone; *n.*I, olfactory nerve; *n.*IX, glossopharyngeal nerve; *n.*X, vagus nerve; *n.hy.*VII, hyoideomandibular ramus of facial nerve; *n.o.*, nasal organ; *n.op.*V, ophthalmic ramus of trigeminal nerve; *n.pal.*VII, palatine ramus of facial nerve; *not.*, notochord; *o.l.*, olfactory lobe of brain; *occ.pr.*, occipital process; *oes.*, œsophagus; *op.a.*, ophthalmic artery; *op.c.*, opercular cartilage; *oper.*, opercular bone; *p.br.* 1–4, first to fourth pharyngobranchial cartilages; *p.orb.*, postorbital cartilage; *p.p.q.*, palatoquadrate cartilage; *p.s.c.*, posterior semicircular canal; *p.s.sp.*, posterior semicircular septum; *pa.p.*, parotic process; *par.*, parachordal cartilage; *pect.*, pectoral fin; *pmx.*, præmaxillary bone; *pr.ot.*, prootic cartilage; *ps.b.*, parasphenoid bone; *ps.br.*, pseudobranchial cartilage; *pty.pr.*, pterygoid process of quadrate cartilage; *q.*, quadrate cartilage; *r.*, rostrum; *r.pal.*, palatine ramus of facial nerve; *rct.p.*, process for attachment of rectus eye-muscles; *rt.p.*, retroarticular process of Meckel's cartilage; *s.o.b.*, supraorbital bar; *s.o.m.*, superior oblique eye-muscles; *s.r.m.*, superior rectus eye-muscles; *sac.*, sacculus; *scl.*, sclerotic cartilage; *sp.c.*, spiracular canal; *sym.*, symplectic cartilage; *sym.p.*, symplectic process of hyomandibular; *t.*, tooth in lower jaw; *t.syn.*, synotic tectum; *tr.*, trabecula cartilage; *tr.c.*, trabecula communis; *utr.*, utriculus.